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Publication dates:

No. 1/2: 30 June, 2005, No. 3/4: 30 December, 2005

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Bonner zoologische Beiträge

Herausgegeben vom

Zoologischen

Forschungsmuseum

Alexander Koenig,

Bonn

In memoriam
Clas M. NAUMANN
(1939-2004)

Band
53
Heft 1/2
2005 (2004)

Leibniz
Gemeinschaft

Ministerium für
Wissenschaft und
Forschung des Landes
Nordrhein-Westfalen
NRW.

Bonner zoologische Beiträge werden publiziert im Eigenverlag Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn (Germany)

Die Zeitschrift erscheint mit vier Heften im Jahr, zum Preis von 11,50 € je Heft bzw. 46,- € je Band incl. Versand. Korrespondenz betreffend Abonnement, Kauf oder Tausch bitten wir zu richten an die Bibliothek, Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn (Germany). E-mail: d.steinebach.zfmk@uni-bonn.de.

© Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn, Germany

ISSN 0006-7172

Druck: Druck Center Meckenheim

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Bonner zoologische Beiträge | Band 53 (2004) | Heft 1/2 | Seiten 1–11 | Bonn, Juni 2005

Clas M. Naumann (26.06.1939 – 15.02.2004) – in memoriam

After several years of suffering from cancer, Professor Clas Michael Naumann zu Königsbrück died on Sunday, 15th of February, 2004. He was a full professor of Systematic Zoology at the Rheinische Friedrich-Wilhelms-Universität and director of the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn.

Fig. 1. Professor Clas Michael Naumann zu Königsbrück, June 12, 1995 (Photo M. Schmitt)

Clas Michael Naumann zu Königsbrück was born the 26th of June 1939, in Dresden as the only child of Dr. Eberhard Naumann zu Königsbrück and Freda-Irene, née Hannemann. He spent the first years of his life at the family estate (Königsbrück, near Dresden) from where he could hear and see the bombing of Dresden (13th/14th of February 1945), an impression he preserved well, as he recounted some fifty years later. He fled from the approaching Red Army with his family in Spring 1945, another experience which left a lasting impression.

His family found a provisional home in the village of Kirchohsen near Hameln, where Clas Naumann entered primary school. From 1949, he went to high school in Wilhelmshaven for two years, and finally in Braunschweig, where his father, who had a doctoral degree in agriculture, found a position with the Bundesforschungsanstalt für Landwirtschaft (Federal Research Institute of Agriculture). From his father, who was an ardent beetle collector, he was guided into natural history. Already during his high school years, he made contact with local entomologists, especially lepidopterists, e.g. Fritz Hartwieg. Certainly through these contacts, Clas Naumann's passion for butterflies and moths developed in those years. He even wrote as his first publication a short report on the Lepidoptera found in the surroundings of Maria Taferl in Austria, where he had spent a summer holiday with his parents (in 1958, no. 1). In 1959, he passed the final secondary-school examinations. After three trimesters of "*studium generale*" at Leibniz Kolleg, Tübingen, he studied chemistry from 1960 to 1962, and biology from 1962 to 1966 at the Eberhard-Karls-Universität in Tübingen. Here, his entomological interests focussed on Burnet Moths, especially of the genus *Zygaena*.

During his time in Tübingen, he undertook his first entomological trip through a country of the Near East, and subsequently published his first species description: *Zygaena problematica* Naumann, 1966, from southern Turkey (no. 2). He also made first experiences as a businessman since he founded a trade of entomology supply. In his later days, he used to tell about this era of his life with great delight.

In 1967, he switched to the Rheinische Friedrich Wilhelms-Universität in Bonn. Here, he received his doctoral degree in 1970 after doing his doctoral dissertation at the Zoologisches Forschungsinstitut und Museum Alexander Koenig on the systematics and phylogeny of the holarctic Sesiidae – Insecta, Lepidoptera, under the supervision of Günther Niethammer (published in 1971, no. 6). Subsequently, he took up an opportunity to work for three years as a university docent at Kabul University (Afghanistan). Besides his teaching, he built up a zoological collection and a small university museum of zoology. The three years he spent in Afghanistan were most influential upon his further life and scientific career. He took more than just a fancy for the nature, culture, history and people of that country. He learned the language(s) of this country and did extensive field work, even in quite remote parts of the country, such as Nuristan and Registan, the provinces of Badakhshan and Paktia, as well the Wakhan Valley in the Afghan Pamirs (Naumann 1974, nos. 11–14). His strong affection for Afghanistan and the whole region of the Middle East lasted for the rest of his life.

He returned to Bonn in 1973 and received a two-year post as an assistant at the Institute for Applied Zoology (Professor Dr. Werner J. Kloft) in Bonn, followed by three years at the Ludwig-Maximilians-Universität in München (Zoological Institute, Professor Dr. Jürgen Jacobs), where he received his habilitation in 1977. His Habilitationsschrift (professorial dissertation) was on the phylogeny and zoogeographical relations of the Zygaenini, published also in English in 1977 (no. 21). The same year he was appointed a professor at Bielefeld University, where he chaired the Department of Morphology and Systematics of Animals until 1989. He continued working on morphology, taxonomy, phylogeny and zoogeography of the Zygaenidae, but extended his field of work into chemical ecology and sensory physiology. A quickly growing number of enthusiastic diploma and doctoral students soon formed a vivid and prolific team of investigators and authors.

On July 1, 1989, he was appointed a full professor at the Rheinische Friedrich Wilhelms-Universität in Bonn, and at the same time director of the Zoologisches Forschungsinstitut und Museum Alexander Koenig. Under his directorship, a corporate plan was elaborated that provided the institution with an internal structure, i.e. departments (vertebrates, entomology, exhibition and public relations) and sections. He initiated monthly scientists' meetings, weekly informal meetings of all staff members, and he made the regular meeting of the heads of the three departments an effectively working and well-accepted board of directors. His main goals were to increase the scientific output and to improve the international standing of Museum Koenig, and to enhance its attractiveness to the public. In all of these activities and throughout the whole of his decisions as Director, he strove for a consensus among the parties involved. And it caused literally anguish to him when he did not succeed in reaching consensus.

Clas Naumann clearly saw that the museum's infrastructure had to be improved drastically in order to reach his goals. So, he worked inconceivably hard to acquire additional funds, be it for additional technical equipment such as a scanning electron microscope or a bone-degreasing device, or for a total renovation of the museum's basement, or for the redesign of its public exhibition. Under his guidance, an entirely new concept for the exhibition was elaborated. With a considerable amount of "soft" money, the reorganisation of the exhibition was achieved, at least partially, before his untimely death. However, most tragically, he was already too feeble to attend the opening ceremony for the first redesigned portion of the exhibition, on the 9th of October 2003.

One of his most notable merits for Museum Koenig was that he succeeded in reaching an administrative decision from the state of Nordrhein-Westfalia and the German Federal Government for a new building. He would definitely not have succeeded without the recruitment to accept a position of full professor at the München University and at the same time director of the Zoologische Staatssammlung München. When negotiating with both the state ministries of Bavaria and Nordrhein-Westfalia, he managed to convince the government of the latter state to guarantee a new building, which would entice him to remain in Bonn. He was intensively involved in the detailed planning and invested a good deal of hope and energy in this enterprise. However, the construction of this new building began only the day after he died.

As a director, Clas Naumann was always concerned about the welfare of the museum's staff members, the countless colleagues who worked at the museum on grants, and of the students doing their theses at the museum. And while he mostly did not show much of his emotions, he could be as merry as a lark when he managed to do something good to somebody, especially when it came as a surprise. Possibly, these were the most rewarding moments in his daily work.

Clas Naumann was a dedicated academic teacher who also stimulated younger scientists to give university courses. In many cases, he announced these courses only formally, while in fact they were given by his doctoral students. Thus, he not only provided these younger colleagues the opportunity of gaining experience in teaching, but also considerably enhanced the range of courses for students of zoology at the Bonn University. In addition, he supervised numerous diploma- and doctoral theses (see list below), both at Bielefeld and Bonn.

Systematists in Central Europe, zoologists and especially museum entomologists, owe Clas Naumann a great deal for his never ending efforts for a better lobby for our field of science within Germany's political and general scientific frame. He was one of the promoters of the Gesellschaft für biologische Systematik (Society for Biological Systematics) founded December 12, 1997, and organised its first annual meeting at Museum Koenig in 1998. He strove for more co-operation between the German museums with vast holdings of scientific collections, was one of the founders of the DNFS (Direktorenkonferenz Naturwissenschaftlicher Forschungssammlungen in Deutschland), and he served for several years as a referee for the Deutsche Forschungsgemeinschaft (German Research Foundation). Through his tireless lobbying, his own scientific papers and through the numerous diploma and doctoral theses he stimulated and supervised, Clas Naumann contributed immensely to the revitalisation and the expansion of taxonomy and systematics in Germany.

Among Clas Naumann's super-regional scientific activities, his efforts for the journal Zoologischer Anzeiger played an outstanding part. He was editor-in-chief since 1995. Without his energy and optimism, this journal would certainly have ended in 1994, when Dr. Johanna Schlüter from Gustav Fischer Verlag, Jena (the publishers at that time) asked Professor Naumann to accept the task of saving the oldest German zoological journal. The present profile of the journal and the boards of editors and advisors still bear Professor Naumann's mark.

Also, Clas Naumann was very much interested in improving the museum's own publication series. It was his explicit desire that Bonner zoologische Beiträge should grow into an internationally renowned, fully peer reviewed journal of high standards in appearance and content. We, the team of editors and advisors since volume 51, are proud to say that Clas Naumann was highly satisfied when he saw the newly designed issues of vol. 51.

Clas Naumann worked tremendously hard for the good of Museum Koenig, for all the persons working here, for a better standing of the science region of Bonn in a wider context, for taxonomy and systematics, and for science in general. He did so finally at the cost of his private life and even his health. Who ever knew him well enough to be able to judge, and close enough to care, felt relieved when he informed us about his decision to retire ahead of schedule in April 2004, and he and we hoped he had some time to devote to his family and his hobbies. But regrettably, he passed away some two months before that date. Thus, he could neither live to see the new building being completed nor could he introduce his successor smoothly into his duties, as he wished.

Two fields of interest absorbed Clas Naumann especially besides his scientific and administrative work: Burnet Moths and Afghanistan (and adjacent countries). In his spare time and on several expeditions, he collected and investigated Zygaenidae. It was one of his highest satisfactions to discover a new species or to rediscover a lost one. He published numerous taxonomic, morphological and zoogeographical studies on that group of moths, and he enjoyed meeting other Zygaenidae enthusiasts (Fig. 2).

Until the last weeks of his life, he was very much concerned about the political, social and scientific developments in Afghanistan, especially at the University of Kabul. While many of his public lectures were either characterised by a certain scientific distance or by tactical considerations (e.g., in order to convince his audience of a certain goal), he gave an entirely different impression when giving a talk on countryside, people, culture and history of Afghanistan. His voice, his smile, his gesture changed. No doubt was left that this was his true passion. He was significantly involved in the revitalisation of the partnership between the Rheinische Friedrich-Wilhelms-Universität Bonn and the Kabul University, and he invested not only just some thoughts in writing several proposals, but he travelled to Kabul and after returning organised campaigns for assistance.

Fig. 2. Clas Naumann on the Isle of Skye (Scotland), during an International Zygaenidae Symposium, September 11, 1996. Left: Gerhard Tarmann (Innsbruck), right: Jean-Marie Desse (Angers) (Photo C. Esch, Münster).

Scientists, technicians, other staff members and students of the Zoologisches Forschungsmuseum Alexander Koenig are deeply indebted to Clas Naumann for his tireless efforts. The board of directors and scientific staff unanimously decided to dedicate the new building to the memory of their former director and to name it "Clas M. Naumann-Bau".

Clas Michael Naumann zu Königsbrück is survived by his wife Storai Naumann-Nawabi and his children Roxana and Alexander, to whom we express our deep sympathy.

Acknowledgements. Storai Naumann-Nawabi (Wachtberg-Pech) read the manuscript of this obituary and relinquished a list of her husband's publications to me, Renate Feist (Bielefeld) compiled a list of Clas Naumann's diploma and doctoral students in Bielefeld, Christoph Häuser (Stuttgart) provided me with a draft of an extensive necrology meant for a lepidopterists' journal, Christoph Esch (Münster) gave permission to use the photograph of Figure 2, Axel Hofmann (Breisach) identified the persons showed on this photo, and Brad Sinclair (Bonn) improved the English of my manuscript.

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Bonner zoologische Beiträge	Band 53 (2004)	Heft 1/2	Seiten 13–26	Bonn, Juni 2005

Neuropterologische Beiträge in den Werken von Wilhelm Friedrich VON GLEICHEN, genannt RUSSWORM (1717-1783)[1]

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Abstract. Among VON GLEICHEN's publications on various topics in zoology, botany, agriculture, and technology there are also three, each of them dealing with a single species of Neuroptera, two appeared in 1764, the third one in 1770. Due to the careful descriptions, and in particular due to the brilliant hand-coloured copper plate engravings, all three species can be identified: *Chrysopa pallens* (Rambur, 1838) (Chrysopidae) (eggs, larva), *Chrysoperla carnea* (Stephens, 1836) (Chrysopidae) (adult), and *Drepanepteryx phalaenoides* (Linnaeus, 1758) (Hemerobiidae) (larva, pupa, adult). None of them has been named by VON GLEICHEN with nomenclaturally available names. The illustrations in the two articles of 1764 are the first figures of Chrysopidae in the whole scientific literature which can be identified on the species level. The figures of the imago of *Ch. carnea*, and of the larva and adult of *D. phalaenoides* are the largest ones ever published.

Key words. Neuroptera, early illustrations, *Chrysoperla carnea, Chrysoperla pallens, Drepanepteryx phalaenoides*, W.F. VON GLEICHEN-RUSSWORM.

1. EINLEITUNG UND BIOGRAPHISCHES

Wilhelm Friedrich VON GLEICHEN, genannt RUßWORM, hat in der Geschichte der Biologie und nicht zuletzt auch der Medizin vor allem durch seine 1778 veröffentlichte „Abhandlung über die Saamen- und Infusionsthierchen, und über die Erzeugung, nebst mikroskopischen Beobachtungen des Saamens der Thiere in verschiedenen Infusionen" eine bleibende Spur hinterlassen. Es handelt sich dabei um ein Werk, das für das Verständnis der Funktion der Spermien von grundlegender Bedeutung war.

In bibliographischen Beschreibungen zu Werken von Wilhelm Friedrich VON GLEICHEN findet man regelmäßig die Feststellung, dass er als erster Bakterien gefärbt hat. Vermutlich gehen alle diese Behauptungen auf einen tradierten Hinweis in Morton's Medical Bibliography (NORMAN 1993) zurück, wo es heißt „GLEICHEN was probably the first to attempt to stain bacteria; he used carmine and indigo". Es ist uns (bisher) weder gelungen, in seinen Schriften sein „Färbe-Rezept" zu finden noch diese Behauptung zu bestätigen. Jedenfalls hat VON GLEICHEN Fütterungsversuche mit Ciliaten unter Verwendung wasserlöslicher Farbstoffe durchgeführt (AESCHT 2004).

Wilhelm Friedrich Freiherr VON GLEICHEN wurde am 14. Jannuar 1717 in Bayreuth geboren. Sein Vater, Heinrich VON GLEICHEN, war „Hochfürstl.-Brandenburgisch-Kulmbachischer Geheimderath und Oberjägermeister" (Anonymus 1784), seine Mutter eine geborene von RUßWORM aus dem Hause Greiffenstein (Der Name wird in manchen Publikationen VON GLEICHENs mit einem, in anderen mit zwei f geschrieben), zu dem das Dorf Bonnland (südlich von Hammelburg in Unterfranken) gehörte.

„Der Knabe, bei dem Markgraf Wilhelm Pate gestanden hatte, erhielt die höfische Erziehung seiner Zeit. In seinem elften Jahr konnte er seinen Namen kaum schreiben" (WILLNAU 1926). Möglicherweise dies und jedenfalls längere Aufenthalte bei verschiedenen aristokratischen Verwandten und Freunden in seiner Kinderzeit waren auf die zerrüttete Ehe seiner Eltern zurückzuführen. Er wurde Page am Taxisschen Hof in Frankfurt, und in seinem 14. Lebensjahr begann seine überaus erfolgreiche militärische Laufbahn (1740, also im Alter von 23 Jahren, war er Major, 1748 Oberstleutnant), die er jedoch 1756 aus „freien Stücken" da er „das Hofleben mit seiner Unruhe, seinem Pomp, Luxus und seiner Intrigue recht satt bekommen" (Bei allen wörtlichen Zitaten haben wir die ursprüngliche Schreibweise und Interpunktion belassen) hatte (WILLNAU 1926) – beendete, um sich auf sein Schloss Greiffenstein zurückzuziehen. VON GLEICHEN muss den Mangel an geistiger Ausbildung in seiner Kindheit inzwischen reichlich wettgemacht haben, und geistige Aktivität kennzeichneten auch sein weiteres Leben, das immerhin noch 27 Jahre dauern sollte. 1748 war seine Mutter gestorben, wo-durch ihm Schloss Greiffenstein und die umliegenden Ländereien zugefallen waren; damals nahm er auch den Namen RUẞWORM an. Sein Vermögen ermöglichte es ihm, sich nun ganz seinen Interessen zu widmen. Ein Schlüsselerlebnis war die Begegnung mit den „Mikroskopischen Augen- und Gemütsergötzungen" von Martin Frobenius LEDERMÜLLER und schließlich mit dem Autor dieses bis heute berühmten Werkes selbst. W. F. VON GLEICHEN besuchte M. F. LEDERMÜLLER 1760 in Erlangen und bestellte bei ihm ein Mikroskop, und Mikroskope sollten fortan auch zu seinen wichtigsten Arbeitsbehelfen gehören. Im Jahre 1762 hielt sich LEDERMÜLLER etwa vier Wochen bei VON GLEICHEN auf Schloß Greiffenstein auf, die beiden Mikroskopiker verbrachten offenbar eine glückliche Zeit, in der sie sich in gemeinsam erlebter Freude und Begeisterung ganz dem Mikroskopieren hingaben. Schon vor seiner Begegnung mit M. F. LEDERMÜLLER, unmittelbar nachdem er sich auf sein Schloss zurückgezogen hatte, hatte W. F. VON GLEICHEN eine rege Publikationstätigkeit begonnen, wobei er sich mit ganz unterschiedlichen naturwissenschaftlichen, landwirtschaftlichen und technischen Fragen befasste. Dass besonders diese frühen Publikationen manchmal eine genügend kritische Betrachtungsweise vermissen lassen, darf nicht unerwähnt bleiben. Ab 1760 wurde W. F. VON GLEICHEN ein Mikroskopiker ersten Ranges, ausgestattet mit einer ausgeprägten Beobachtungsgabe und einer ebenso ausgeprägten Lust, das Gesehene zu interpretieren, Schlüsse zu ziehen und zu veröffentlichen. So entstanden zahlreiche weitere Publikationen über sehr unterschiedliche naturwissenschaftliche Themen (Bibliographie: FIKENSCHER 1801).

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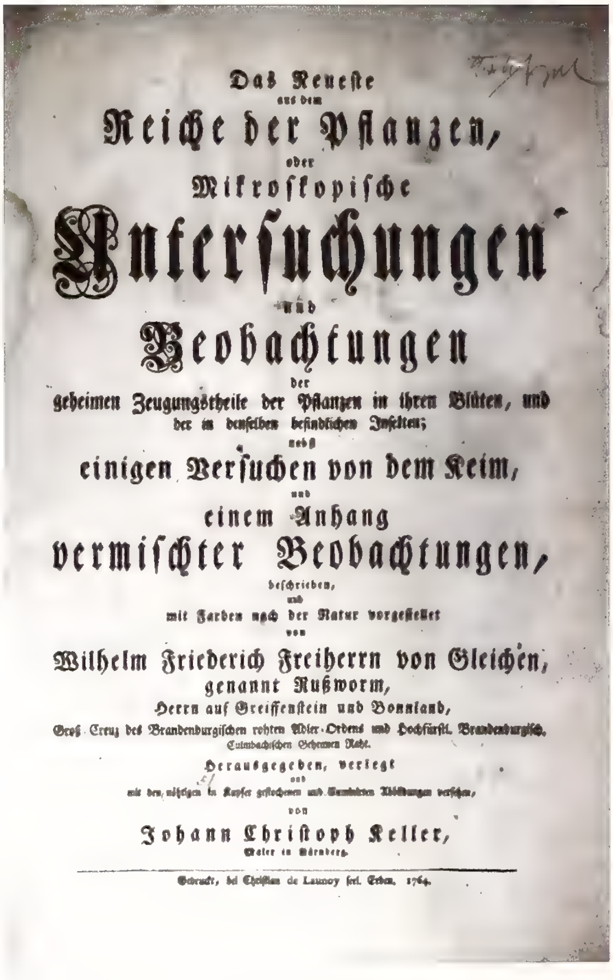
[1] Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004) zum Gedenken

W. F. VON GLEICHEN starb infolge eines Schlaganfalls in seinem 67. Lebensjahr am 16. (oder 18.) Juni 1783 auf Schloss Greiffenstein.

Die Bedeutung W. F. VON GLEICHENs als Naturforscher wurde schon zu seinen Lebzeiten erkannt, und schon unmittelbar nach seinem Tod erschienen Darstellungen seines Lebenswegs: WEIKARD 1783; ANONYMUS 1784; FIKENSCHER 1801. Von den späteren biographischen Publikationen über W. F. VON GLEICHEN sind vor allem die Arbeiten von WILLNAU (1926), WEIDNER (1980), GEUS (1989, 1990) und DETTNER (1997) zu erwähnen.

W. F. VON GLEICHEN war nicht nur ein begabter Experimentator, sondern ein ebenso talentierter Zeichner, der seine Publikationen mit vorzüglichen Abbildungen ausstattete. Seine berühmteste und durch hervorragend kolorierte Kupfertafeln ausgestattete entomologische Arbeit ist ohne Zweifel jene über die „Geschichte der gemeinen Stubenfliege" (VON GLEICHEN 1764), in der er überdies Beobachtungsfehler von M. F. LEDERMÜLLER aufzeigte, was bedauerlicherweise zu einer Entzweiung der beiden führte.

Entomologische Themen werden auch in mehreren anderen Publikationen VON GLEICHENs behandelt. In zwei Werken setzt sich VON GLEICHEN mit Neuropteren auseinander, nämlich in dem 1764 erschienene Band über „Das Neueste aus dem Reiche der Pflanzen ..." (Abb. 1) und in seinem 1770 publizierten „Versuch einer Geschichte der Blatläuse und Blatlausfreßer des Ulmenbaums ..." (Abb. 9). Das 1764 veröffentlichte Werk ist – wie man schon dem langen Titel („... und einem Anhang vermischter Beobachtungen ...") entnehmen kann – so etwas wie ein Sammelband über verschiedene Themen. Er enthält auch zwei neuropterologische Artikel, von denen der eine („Der Blatlausfreßer und seine Eier an einem Hanfblat") den präimaginalen Stadien einer Chrysopiden-Spezies, der andere („Die Hofdame") einer im Winter gefundenen Imago einer Florfliege gewidmet ist.



Das Neueſte
aus dem
Reiche der Pflanzen,
oder
Mikroſkopiſche
Unterſuchungen
und
Beobachtungen
der
geheimen Zeugungstheile der Pflanzen in ihren Blüten, und
der in denſelben befindlichen Inſekten;
nebſt
einigen Verſuchen von dem Keim,
und
einem Anhang
vermiſchter Beobachtungen,
beſchrieben,
und
mit Farben nach der Natur vorgeſtellet
von
Wilhelm Friederich Freiherrn von Gleichen,
genannt Rußworm,
Herrn auf Greiffenſtein und Bonnland,
Groß-Creuz des Brandenburgiſchen rohten Adler-Ordens und Hochfürſtl. Brandenburgiſch-
Culmbachiſchen Geheimen Raht.
Herausgegeben, verlegt
und
mit den nöthigen in Kupfer geſtochenen und illuminirten Abbildungen verſehen,
von
Johann Chriſtoph Keller,
Maler in Nürnberg.

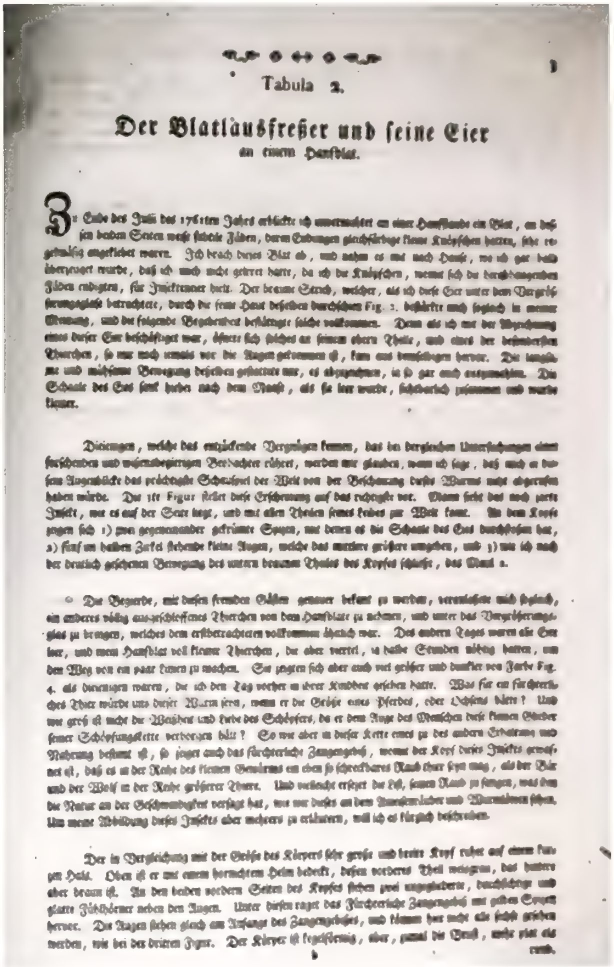
Gedruckt, bei Chriſtian de Launoy ſel. Erben, 1764.

Abb. 1: W. F. VON GLEICHEN (1764), Titelblatt des Werks, das die Arbeiten über den „Blatlausfreßer ..." (1764a) und „Die Hofdame" (1764b) enthält (Bibl. H. & U. ASPÖCK)

In der 1770 veröffentlichten umfangreichen Arbeit wird die Biologie einer Hemerobiiden-Spezies ausführlich dargestellt. VON GLEICHEN hat sich wenig um die korrekte Bestimmung und Benennung der von ihm untersuchten Insekten gekümmert, vielmehr hat er einfache deutsche Namen verwendet. Sein Augenmerk konzentrierte sich ganz und gar auf die funktionellen Aspekte, auf Lebensweise und Entwicklung, während ihn taxonomische und systematisch Aspekte offenbar gar nicht interessierten. Geus (1990) zitiert eine geradezu abfällige Aussage von Gleichens über jene Naturforscher, „die nur Systeme ausheckten, von nichts als Nomenklatur, Papillons, Konchylien u.d.g. mit einem Worte, nur immer von der Schale der Dinge schwatzten. Solche Menschen setzen meistens die Naturkunde nur zu einem blossen Gedaechtniswerke oder blos zu einer leeren Liebhaberei herab.“

2. 1764A: „DER BLATLAUSFREßER UND SEINE EIER AN EINEM HANFBLAT“ (ABB. 2-6)

In diesem Aufsatz schildert von Gleichen, wie er Ende Juli 1761 an einer Hanfstaude ein Blatt fand, „an dessen beiden Seiten weise subtile Fäden, deren Endungen gleichfärbige kleine Knöpfchen hatten, sehr regelmäßig angeklebet waren“. von Gleichen brach das Blatt ab, nahm es mit nach Hause und fand seine Vermutung, dass es sich bei den „Knöpfchen“ um Insekteneier handelte, bestätigt, als er bei Betrachtung der Knöpfchen unter dem Mikroskop die durchscheinende Larve sah und plötzlich Zeuge des Schlüpfens der Eilarve wurde. von Gleichen beschreibt Eier und Larven außerordentlich genau und bildet sie auch in hervorragender Weise ab; seine Zeichnungen dienten Johann Christoph Keller (1737-1795) als Vorlagen für die Kupferstiche (Abb. 2). Zu seinem Bedauern konnte er keine weiteren Zeichnungen anfertigen, weil die Larven nach drei Tagen tot und eingeschrumpft waren. Von Gleichen wusste zu diesem Zeitpunkt nicht, welche Insekten er vor sich hatte, was ihre Nahrung ist, ja er schreibt sogar ganz offenherzig: „Allein meine Ungewissheit ihrer Bestimmung verleitete mich, zu glauben, dass sie wenigstens nicht viel größer werden würden, als sie waren, da ich eines derselben Fig. 4. vergrößert abbildete.“ Erst nach dieser Untersuchung kam von Gleichen das berühmte Werk von Réaumur (1734-1742) in die Hände, in dessen drittem Band (1737) die Biologie von Chrysopiden beschrieben wird. Von Gleichen gibt auch unumwunden zu, dass er, hätte er von Réaumurs Werk vorher Kenntnis gehabt, mit seinen „Blatlausfreßern viel sorgfältiger umgegangen seyn würde“. Erst durch Réaumur erfuhr von Gleichen , dass die „Fresszangen“ nicht zum Fressen, sondern zum Saugen dienen und dass sie „hohl und an den Spitzen offen sind“. Dass diese Saugzangen von größter systematischer Bedeutung sind und das die Ordnung Neuroptera begründende Merkmal schlechthin (also in heutiger Terminologie: die Autapomorphie) der Neuroptera sind, wusste auch Réaumur nicht. Erst mehr als 100 Jahre später erkannte der junge Friedrich Brauer den außerordentlichen systematischen Wert des Merkmals, indem er alle Familien der Neuroptera (im heutigen Sinn) in einer Ordnung (er nannte sie damals Megaloptera) vereinte (Brauer & Löw 1857).



Tabula 2.

Der Blatlausfreßer und ſeine Eier

an einem Hanfblat.

Abb. 2: W. F. von Gleichen (1764a), Erste Seite der Arbeit über den „Blatlausfreßer ...“

Wahrscheinlich verdanken wir indes dem Umstand, dass von Gleichen das Werk von Réaumur nicht früher zur Hand hatte, die schön kolorierte Kupfertafel der Eier und der Erstlarve. (Die auf Fig. 5 und Fig. 6 dargestellten leeren Eier stammen von einem späteren Fund des Gärtners von Gleichens auf einer Zwetschke.) Unseres Wissens handelt es ich dabei um die erste farbige Darstellung einer Chrysopiden-Larve mit einer Wiedergabe des Pigmentierungsmusters in der gesamten entomologischen Literatur. Die Darstellung ist so genau, dass der Versuch, die Larve zu bestimmen, lohnend erschien. Die Larven fast aller in Mitteleuropa vorkommenden Chrysopiden sind gut bekannt, zu überwiegendem Teil existieren auch (allerdings nicht durchwegs

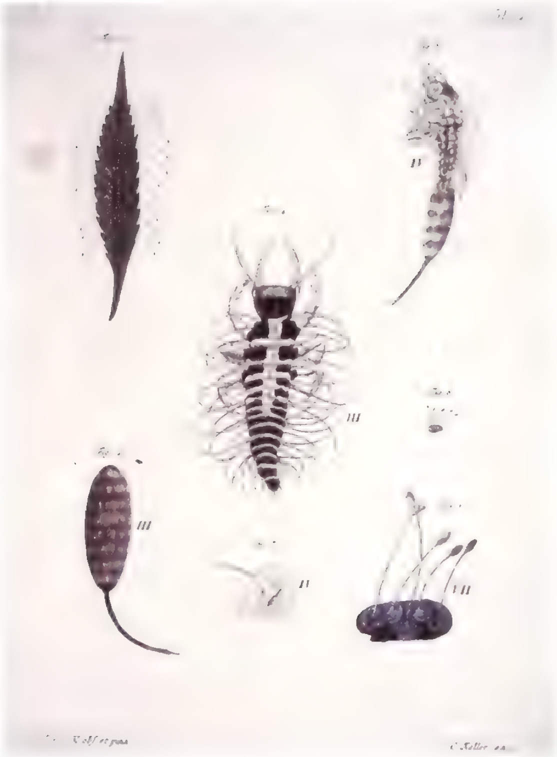


Abb. 3: W. F. VON GLEICHEN (1764a), Tafel zu der Arbeit über den „Blatlausfreßer ...“

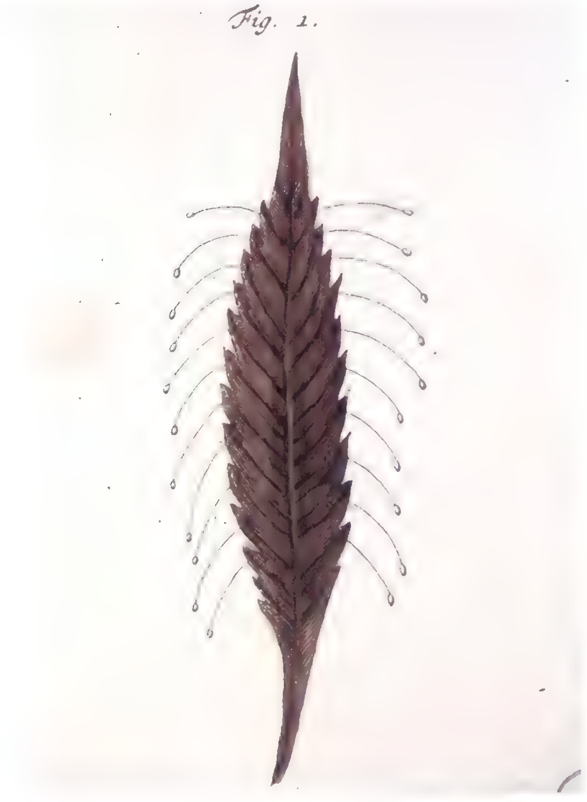


Abb. 4: W. F. VON GLEICHEN (1764a), Ausschnitt der Tafel zu der Arbeit über den „Blatlausfreßer ...“: Die in (für *C. pallens* charakteristischen) Reihen abgelegten Eier.

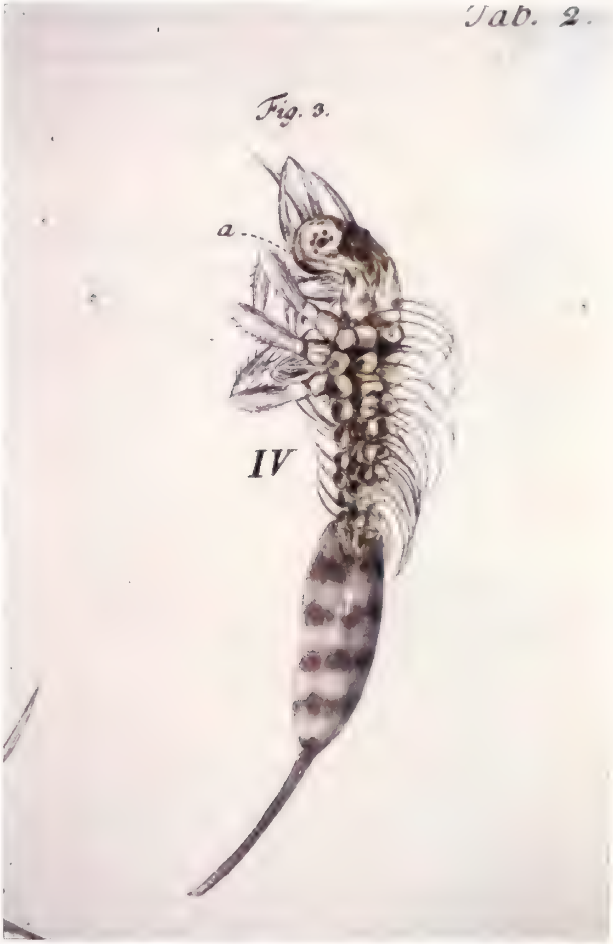

Tab. 2.
Fig. 3.
a
IV

Abb. 5: W. F. VON GLEICHEN (1764a), Ausschnitt der Tafel zu der Arbeit „Blatlausfreßer ...“: Die aus dem Ei schlüpfende Larve (von *C. pallens*).

auch vom ersten Larvenstadium) gute Abbildungen (vgl. KILLINGTON 1936-1937; PRINCIPI 1940; GEPP 1983; DIAZ-ARANDA 1992; DIAZ-ARANDA & MONSERRAT 1995). Vergleicht man die Larve VON GLEICHENS mit den verfügbaren Abbildungen, so findet sich die größte Übereinstimmung mit *Chrysopa pallens* (Rambur, 1838). Wir haben den derzeit vermutlich besten Kenner der präimaginalen Stadien von Chrysopiden, Herrn Prof. Dr. Peter DUELLI (Birmensdorf) um eine Beurteilung der Abbildung in VON GLEICHENs Arbeit gebeten. Nach seiner Meinung lassen die in Reihen abgelegten Eier sofort auf *C. pallens* schließen. Ebenso spricht die Pigmentierung der Kopfkapsel am ehesten für *C. pallens*. Weiters schreibt er: „Die langen, am Ende gebogenen Borsten lassen auf einen trash-carrier schließen. Das ist *C. pallens* ja nicht. Allerdings sind bei allen Chrysopiden-Arten die Borsten des ersten Larvenstadiums, relativ zur Körperlänge gesehen, viel länger als im 3. Larvenstadium. Auch tragen viele Arten dann doch noch etwas trash (debris) mit sich herum, später nicht mehr. Verglichen etwa mit *Chrysoperla*-Larven sind bei *C. pallens* auch bei der L3 die Borsten sehr lang." Zusammenfassend hält Prof. DUELLI die Larven in VON GLEICHENs Arbeit mit größter Wahrscheinlichkeit für *Chrysopa pallens.*

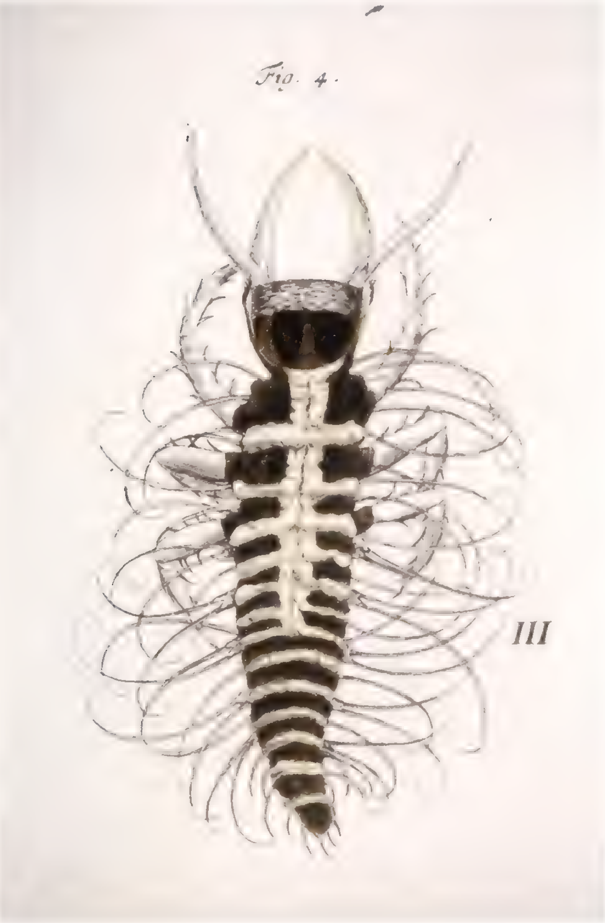


Abb. 6: W. F. VON GLEICHEN (1764a), Ausschnitt der Tafel zu der Arbeit über den „Blatlausfreßer ....": Erstlarve (von *C. pallens*).

Diese Art (früher als *Chrysopa septempunctata* Wesmael, 1841, bekannt) ist eine extrem expansive, polyzentrische Art mit Ausbreitungszentren in der West- und in der Ostpaläarktis und einer Verbreitung, die nahezu ganz Europa (mit Ausnahme der nördlichen Teile, jedenfalls ganz Mitteleuropa von der Ebene bis in die kolline Stufe), NW-Afrika sowie weite (auch tropische) Teile Asiens östlich bis Japan und Taiwan umfasst (ASPÖCK et al. 1980; ASPÖCK et al. 2001). Mit Sicherheit war und ist die Art im Bereich des RUßWORM'schen Schlosses, wie überhaupt in Franken, häufig. (Zur Verbreitung von *Ch. pallens* in Deutschland siehe SAURE et al 2003.)

Diese durch die erste kenntliche Farbabbildung einer Chrysopiden-Larve und die Beschreibung des Schlüpfvorgangs bemerkenswerte Arbeit VON GLEICHENs ist offenbar weitestgehend in Vergessenheit geraten. Selbst in der an Vollständigkeit kaum überbietbaren Bibliographie von OSWALD (2004) fehlt sie. Ältere und z. T. sogar kolorierte Darstellungen von Chrysopiden-Larven finden sich u. a. bei GOEDART (1669), ALBIN (1720), FRISCH (1736), RÉAUMUR (1734-1742), BONNET (1745, Übersetzung: GOEZE 1773), sie sind allerdings durchwegs grob ausgeführt und lassen jedenfalls keine Art-Bestimmung zu.

3. 1764B: „DIE HOFDAME" (ABB. 7-8)

Auch diese Arbeit mit dem ungewöhnlichen Titel fehlt in der Bibliographie von OSWALD (l. c.), obwohl sie die vermutlich größte je publizierte Abbildung einer Chrysopide enthält.

VON GLEICHEN schildert in dem der Zeit entsprechenden narrativen Stil, wie sich „zur Zeit des Carnevals im Jenner bei später Nacht" ein Insekt auf eine Spielkarte setzte, das durch seine Schönheit auffiel (weshalb ihm VON GLEICHEN den Namen „Hofdame" gab). Tags darauf untersuchte VON GLEICHEN das Insekt mit freiem Auge ebenso wie unter dem Mikroskop und führte eine kolorierte Zeichnung aus, von der J. C. KELLER einen Kupferstich anfertigte, den VON GLEICHEN kolorierte.

Das Insekt ist von jedem Entomologen sogleich als Chrysopide zu erkennen, und jeder Neuropterologe weiß, dass es sich dabei nur um eine *Chrysoperla*-Art handeln kann. Die in Mitteleuropa vorkommenden Chrysoperla-Arten überwintern als Imagines, und unter diesen nehmen manche (in Mitteleuropa als einzige Chrysopiden) im Herbst eine gelblich-bräunlich-rötliche Färbung an. Vor 40 Jahren wäre die Bestimmung völlig problemlos erschienen. Damals kannte man nur eine einzige Chrysopiden-Spezies unter den Chrysopiden Mitteleuropas, die als Imago überwintert und im Herbst ihre Färbung von grün in braun verändert: *Chrysoperla carnea* (Stephens, 1836). Im Verlauf der vergangenen Jahrzehnte hat sich gezeigt, dass „die alte *Chrysoperla carnea*" nur als Kollektivnahme für mehrere morphologisch schwierig zu differenzierende Spezies zu betrachten ist, von denen mindestens 5 in Europa und z. T. auch in Mitteleuropa vorkommen (Literatur hierzu: HENRY & DUELLI 1999; HENRY et al 1996, 2002; HENRY et al 2003; JOHNSON et al 2003; ASPÖCK et al. 2001):

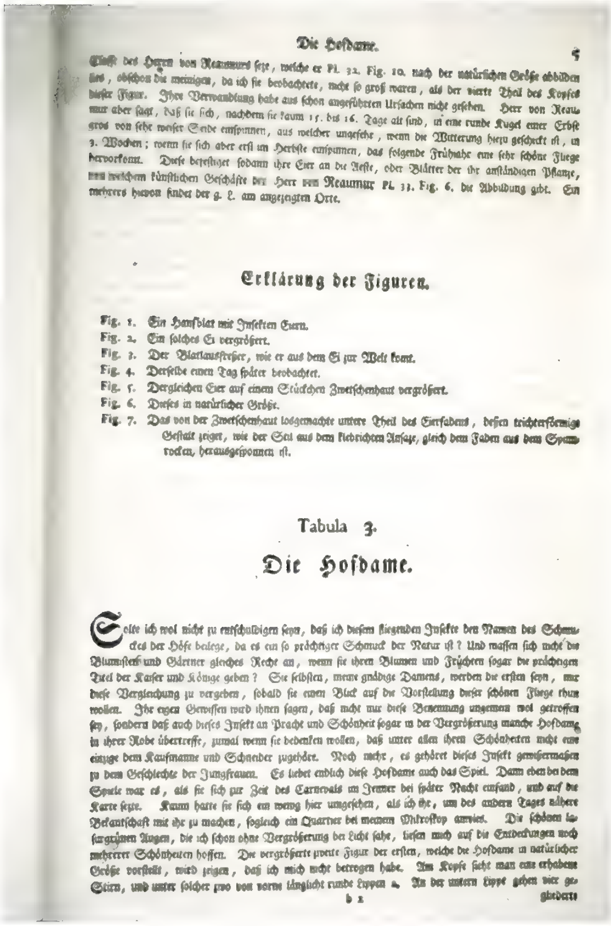
Chrysoperla carnea (Stephens, 1836)

Chrysoperla lucasina (Lacroix, 1912)

Chrysoperla mediterranea (Hölzel, 1972)

Chrysoperla pallida (Henry, Duelli & Johnson, 2002)

Chrysoperla agilis (Henry, Brooks, Duelli & Johnson, 2003).



Die Hofdame. 5

Claſſe des Herrn von Reaumurs ſeze, welche er Pl. 32. Fig. 10. nach der natürlichen Gröſſe abbilden läs, obſchon die meinigen, da ich ſie beobachtete, nicht ſo groß waren, als der vierte Theil des Kopfes dieſer Figur. Ihre Verwandlung habe aus ſchon angeführten Urſachen nicht geſehen. Herr von Reaumur aber ſagt, daß ſie ſich, nachdem ſie kaum 15. bis 16. Tage alt ſind, in eine runde Kugel einer Erbſe gros von ſehr weiſer Seide einſpinnen, aus welcher ungefehr, wenn die Witterung hiezu geſchickt iſt, in 3. Wochen; wenn ſie ſich aber erſt im Herbſte einſpinnen, das folgende Frühjahr eine ſehr ſchöne Fliege hervorkomt. Dieſe befeſtiget ſodann ihre Eier an die Aeſte, oder Blätter der ihr anſtändigen Pflanze, von welchem künſtlichen Geſchäfte der Herr von Reaumur Pl. 33. Fig. 6. die Abbildung gibt. Ein mehreres hievon findet der g. L. am angezeigten Orte.

Erklärung der Figuren.

Fig. 1. Ein Hanfblat mit Inſekten Eiern.
Fig. 2. Ein ſolches Ei vergröſſert.
Fig. 3. Der Blatlausfreſſer, wie er aus dem Ei zur Welt komt.
Fig. 4. Derſelbe einen Tag ſpäter beobachtet.
Fig. 5. Dergleichen Eier auf einem Stückchen Zwetſchenhaut vergröſſert.
Fig. 6. Dieſes in natürlicher Gröſſe.
Fig. 7. Das von der Zwetſchenhaut losgemachte untere Theil des Eierfadens, deſſen trichterförmige Geſtalt zeiget, wie der Seil aus dem klebrichten Anſaze, gleich dem Faden aus dem Spinnrocken, herausgeſponnen iſt.

Tabula 3.

Die Hofdame.

Solte ich wol nicht zu entſchuldigen ſeyn, daß ich dieſem fliegenden Inſekte den Namen des Schmuckes der Höfe beilege, da es ein ſo prächtiger Schmuck der Natur iſt? Und maſſen ſich nicht die Blumiſten und Gärtner gleiches Recht an, wenn ſie ihren Blumen und Früchten ſogar die prächtigen Titel der Kaiſer und Könige geben? Sie ſelbſten, meine gnädige Damens, werden die erſten ſeyn, mir dieſe Vergleichung zu vergeben, ſobald ſie einen Blick auf die Vorſtellung dieſer ſchönen Fliege thun wollen. Ihr eigen Gewiſſen wird ihnen ſagen, daß nicht nur dieſe Benennung ungemein wol getroffen ſey, ſondern daß auch dieſes Inſekt an Pracht und Schönheit ſogar in der Vergröſſerung manche Hofdame in ihrer Robe übertreffe, zumal wenn ſie bedenken wollen, daß unter allen ihren Schönheiten nicht eine einzige dem Kaufmanne und Schneider zugehöre. Noch mehr, es gehöret dieſes Inſekt gewiſſermaſſen zu dem Geſchlechte der Jungfrauen. Es liebet endlich dieſe Hofdame auch das Spiel. Denn eben bei dem Spiele war es, als ſie ſich zur Zeit des Carnevals im Jenner bei ſpäter Nacht einfand, und auf die Karte ſezte. Kaum hatte ſie ſich ein wenig hier umgeſehen, als ich ihr, um des andern Tages nähere Bekantſchaft mit ihr zu machen, ſogleich ein Quartier bei meinem Mikroſkop anwies. Die ſchönen lasurgrünen Augen, die ich ſchon ohne Vergröſſerung bei Licht ſahe, lieſen mich auf die Entdeckungen noch mehrerer Schönheiten hoffen. Die vergröſſerte zweite Figur der erſten, welche die Hofdame in natürlicher Gröſſe vorſtellt, wird zeigen, daß ich mich nicht betrogen habe. Am Kopfe ſieht man eine erhabene Stirn, und unter ſolcher zwo von vorne länglicht runde Lippen a. An der untern Lippe gehen vier ge-

b 2 gliederte

Abb. 7: W. F. VON GLEICHEN (1764b), erste Seite der Arbeit über „Die Hofdame“.

Diese fünf Taxa unterscheiden sich vor allem durch spezifische Vibrationsmuster, die sich durch verschieden langes, durch unterschiedliche Intervalle und Folgen gekennzeichnetes Vibrieren mit dem Abdomen ergeben. Die Vibrationen werden auf das Substrat übertragen und erreichen über dieses andere Individuen, die die spezifischen Signale mit den Subgenualorganen der Beine wahrnehmen. Beide Geschlechter zeigen dieses der Partner-Findung dienende Verhalten, und wenn zwei Phäna mit unterschiedlichen Vibrationsmustern zusammentreffen, kommt es nicht nur nicht zur Paarung, in vielen Fällen ist sogar eine aggressive Reaktion die Folge. Die Taxa sind Spezies mit zum Teil unterschiedlich fortgeschrittener genetischer Isolierung. Sie werden häufig als „song-morphs“ bezeichnet. Unter experimentellen Bedingungen können Paarungen zwischen verschiedenen „song-morphs“ manchmal „erzwungen“ werden.

Ch. mediterranea und *Ch. lucasina* unterscheiden sich morphologisch hinlänglich und konstant von den anderen drei Spezies, deren morphologische Unterschiede gering sind. Alle genannten *Chrysoperla*-Arten überwintern als Imagines, aber nur drei von ihnen (*Ch. carnea, Ch. pallida, Ch. agilis*) verändern im Herbst die Färbung von grün zu rötlich-bräunlich-gelblich. Diese Färbung wird während der gesamten winterlichen Diapause bis zum nächsten Frühjahr beibehalten. Für die Deutung der Abbildung der „Hofdame“ (Abb. 8) VON GLEICHENs scheiden also *Ch. lucasina* und *Ch. mediterranea* jedenfalls aus.

Auch die in verschiedenen Teilen des Mittelmeerraums nördlich bis in die Südschweiz nachgewiesene *Ch. agilis* kann ausgeklammert werden, sie ist im übrigen bisher in Mitteleuropa nicht nachgewiesen worden und kommt mit großer Wahrscheinlichkeit in diesem Teil Europas tatsächlich nicht vor. Von den verbleibenden zwei Arten – *Ch. carnea* und *Ch. pallida* – gilt *Ch. pallida* als „Waldart“, die nur selten in Häusern überwintert. *Ch. carnea* hingegen ist ein ausgeprägter Kulturfolger und eine in allen Städten und Dörfern Mitteleuropas häufige Florfliege.

Auch in diesem Fall haben wir den führenden *Chrysoperla*-Spezialisten, Prof. Dr. Peter DUELLI (Birmensdorf), um seine Beurteilung des kolorierten Kupferstichs gebeten. Seine Antwort: „Die Färbung der Hofdame ist exakt das, was ich für *C. carnea* s. str. erwarten würde. Auch die Tatsache, dass sie im Januar im Haus anflog, spricht für *carnea*, *C. lucasina* ist wegen der Färbung ausgeschlossen, *C. pallida* (Waldart) kommt selten in die Häuser und ist etwas bräunlich-gelber im Winter“. Wir können also tatsächlich davon ausgehen, dass W. F. VON GLEICHEN die erste kenntliche – und überdies farbige – Darstellung jener Spezies veröffentlicht hat, die STEPHENS (1836) mehr als 70 Jahre später als *Chrysopa carnea* nomenklatorisch gültig beschrieben hat und die mit Sicherheit die in der Literatur am meisten behandelte Neuropteren-Spezies ist. *Chrysoperla carnea* ist zudem gewiss auch die am intensivsten und unter den verschiedensten Gesichtspunkten untersuchte Neuropteren-Art. VON GLEICHENs Abbildung ist – obwohl 240 Jahre alt – keineswegs die erste Abbildung einer Florfliege. Darstellungen von Chrysopiden findet man schon bei MOUFFET (1634), ALDROVANDI (1638), JONSTON (1657), GOEDART (1668), FRISCH (1736), RÖSEL VON ROSENHOF (1755), und natürlich bei RÉAUMUR (1734-1742) und bei BONNET (1745) und anderen früheren Autoren. Einige Autoren (GOEDART, ALBIN, RÖSEL VON ROSENHOF) haben sogar kolorierte Abbildungen veröffentlicht. Allerdings ist eine sichere Identifizierung der Art in keinem Fall möglich. Man muss jedoch gerechterweise erwähnen, dass drei Umstände die Identifizierung der von VON GLEICHEN dargestellten Florfliege ermöglicht haben: die genaue Kenntnis des Fundorts (Schloss Greiffenstein in Unterfranken), das Funddatum (Januar, aktiv im Haus) und die bräunliche (Ver-) Färbung des Tiers. Das Geäder hat VON GLEICHEN zwar sehr schön (und sogar – erstmals in der Literatur – mit doppelten Strichen), aber alles andere als richtig gezeichnet. Zu jener Zeit wusste man natürlich noch nichts über Geäder-Merkmale von Chrysopiden und deren systematische Bedeutung, weshalb man – das gilt geradezu für alle Autoren jener Zeit – auf eine korrekte Wiedergabe des Geäderverlaufs und der Zahl und Position der Queradern kaum achtete.

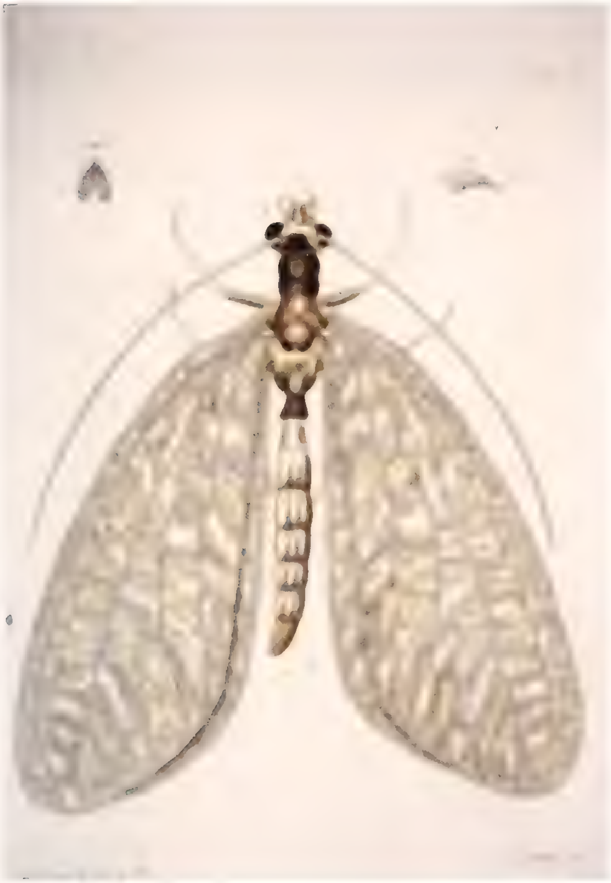


Abb. 8: W. F. VON GLEICHEN (1764b), Tafel zu der Arbeit über „Die Hofdame" (= *Chrysoperla carnea*).

VON GLEICHEN mutmaßte, dass seine „Hofdame" „die nemliche ist, welche nach der Beschreibung des Herrn von RÉAUMURs aus der seidenartigen Puppe hervorkomt". Das ist sicher nicht richtig, aufgrund der biologischen Angaben von RÉAUMUR kann es sich nicht um eine *Chrysoperla*-Art gehandelt haben. Auch VON GLEICHENs Vermutung, dass seine „Hofdame" sich aus einem „entkommenen Blatlausfreßer", der im „Zimmer eine ... anständige Speise" gefunden habe, entwickelt habe und „dass durch die Wärme geheizter Zimmer, wie dies bei allen sich verwandelnden Insekten geschieht, das Wachstum und Auskriechen der Fliege dergestalt befördert worden ist, daß letzteres im Jenner erfolget, da es nach Herrn von RÉAUMUR bei den Spätlingen erst im Frühjahr geschieht.." trifft natürlich nicht zu. RÉAUMUR hat über eine Spezies geschrieben, die nicht als Imago überwintert.

Erstaunlich ist indes, dass VON GLEICHEN offenbar erst kurz vor der Veröffentlichung seines Artikels über die „Hofdame" (er war damals immerhin schon 47 Jahre alt) eine Florfliege beachtet hat, denn nichts in den beiden Artikeln, die sich mit Chrysopiden befassen, deutet darauf hin, dass VON GLEICHEN diese Insekten vorher gekannt hatte. Kaum ein an der Natur und insbesondere an Insekten interessierter Mensch in Mitteleuropa begegnet nicht schon früh, meist irgendwann in der Kindheit, einer Florfliege und erkennt die charakteristischen, in etwa 30 Arten in Mitteleuropa vorkommenden Neuropteren immer wieder. Auch und besonders an den bräunlich verfärbten Florfliegen kann man im Spätherbst, Winter oder Vorfrühling kaum vorübergehen, weil sie in fast allen Häusern, die von Gärten oder gar Feldern umgeben sind, vorkommen; oft findet man sie – besonders in alten Häusern – zwischen Fenstern, wo sie manchmal in Ritzen überwintern.

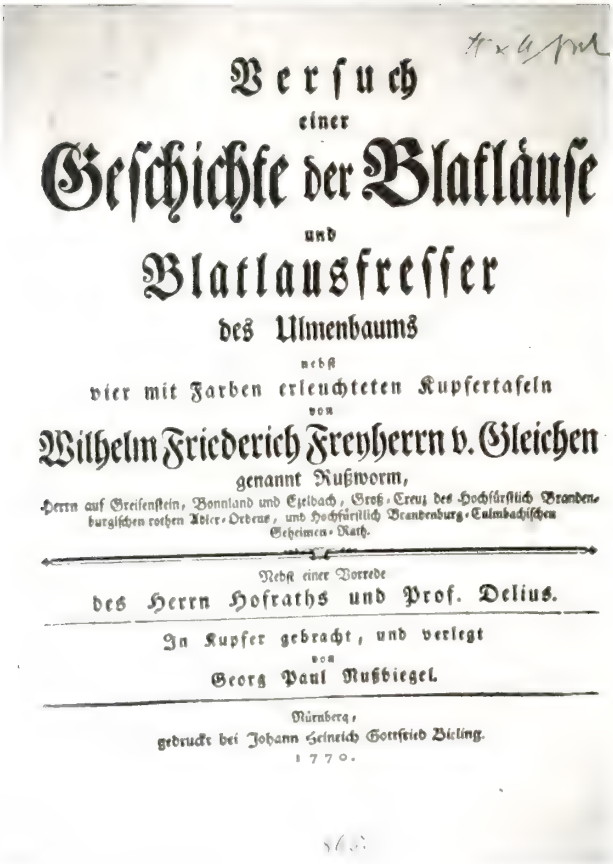
In allen größeren entomologischen Werken, die vor 1764 existierten, sind auch Chrysopiden behandelt und auch abgebildet worden.

Bei aller Würdigung der Verdienste VON GLEICHENs erstaunt es doch, dass ein in einer so sorgenfreien materiellen Situation lebender Mensch mit einer so ausgeprägten Neugierde für die Natur nicht über die entomologischen Standard-Werke, die im 17. und 18. Jahrhundert erschienen waren, verfügte. Er muss demnach zumindest in den ersten Jahren seiner naturwissenschaftlichen Studien auf Schloss Greiffenstein nur eine bescheidene Bibliothek besessen haben.

4. 1770: „VERSUCH EINER GESCHICHTE DER BLATLÄUSE UND BLATLAUSFRESSER DES ULMENBAUMS" (ABB. 9-12)

Diese 1770 und in einer 2. Auflage 1787 erschienene, insgesamt 30 Seiten umfassende und mit vier kolorierten Kupferstichen ausgestattete Publikation zählt zu den bekanntesten Arbeiten des Autors und ist zumindest von MORTON (1910), WEIDNER (1980), GEUS (1989) und DETTNER (1997) besprochen worden. Im Vordergrund der Sekundärliteratur steht der Nachweis des Lebenszyklus und insbesondere der Parthenogenese der Ulmenblattlaus, *Byrsocrypta ulmi* (L.), durch VON GLEICHEN sowie dessen Überlegungen zu diesem Phänomen.

Im Zuge der Befassung mit den Blattläusen stieß VON GLEICHEN auf einen der Prädatoren unter den Neuropteren, jene charakteristische Hemerobiiden-Spezies, die LINNAEUS (1758) als *Hemerobius phalaenoides* beschrieben hat und die später in das Genus *Drepanepteryx* Leach transferiert wurde.



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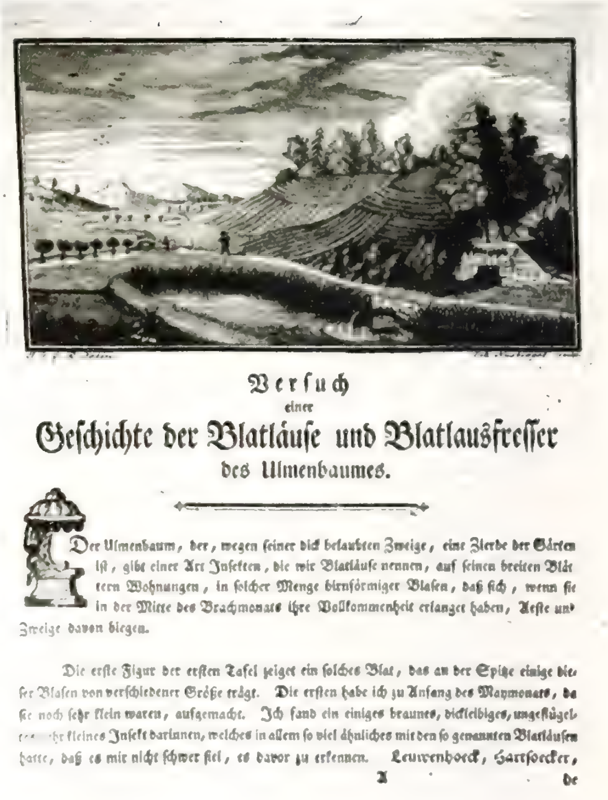
Verſuch
einer
Geſchichte der Blatläuſe
und
Blatlausfreſſer
des Ulmenbaums
nebſt
vier mit Farben erleuchteten Kupfertafeln
von
Wilhelm Friederich Freyherrn v. Gleichen
genannt Rußworm,
Herrn auf Greifenſtein, Bonnland und Etzelbach, Groß-Creuz des Hochfürſtlich Brandenburgiſchen rothen Adler-Ordens, und Hochfürſtlich Brandenburg-Culmbachiſchen Geheimen-Rath.

Nebſt einer Vorrede
des Herrn Hofraths und Prof. Delius.

In Kupfer gebracht, und verlegt
von
Georg Paul Nußbiegel.

Nürnberg,
gedruckt bei Johann Heinrich Gottfried Bieling.
1770.

Abb. 9: W. F. VON GLEICHEN (1770), Titelblatt (Bibl. H.& U. ASPÖCK)



Verſuch
einer
Geſchichte der Blatläuſe und Blatlausfreſſer
des Ulmenbaumes.

Der Ulmenbaum, der, wegen ſeiner dick belaubten Zweige, eine Zierde der Gärten iſt, gibt einer Art Inſekten, die wir Blatläuſe nennen, auf ſeinen breiten Blättern Wohnungen, in ſolcher Menge birnförmiger Blaſen, daß ſich, wenn ſie in der Mitte des Brachmonats ihre Vollkommenheit erlanget haben, Aeſte und Zweige davon biegen.

Die erſte Figur der erſten Tafel zeiget ein ſolches Blat, das an der Spitze einige dieſer Blaſen von verſchiedener Größe trägt. Die erſten habe ich zu Anfang des Maymonats, da ſie noch ſehr klein waren, aufgemacht. Ich fand ein einiges braunes, dickleibiges, ungeflügeltes ſehr kleines Inſekt darinnen, welches in allem ſo viel ähnliches mit den ſo genannten Blatläuſen hatte, daß es mir nicht ſchwer fiel, es davor zu erkennen. Leuwenhoeck, Hartſoecker,

A de

Abb. 10: W. F. VON GLEICHEN (1770), erste Seite (mit der von „J.d.G.R.“ [= J. VON GLEICHEN-RUSSWORM? Ein Verwandter?] gezeichneten und von Johann NUSBIEGEL (1750-1833) gestochenen Vignette.

Etwa sieben Seiten Text und zwei kolorierte Kupferstiche widmet VON GLEICHEN der Beschreibung der Larve und der Imago von *D. phalaenoid*es (Abb. 10 - 12). Die Zeichnungen hat VON GLEICHEN – wie in seinen Werken durchwegs – selbst angefertigt, die Tafeln wurden von seinem Verleger, dem Kupferstecher Georg Paul NUßBIEGEL (um 1713 – 1786), gestochen.

VON GLEICHEN beschreibt, wie er in dem Gewimmel der jungen Blattläuse "einige braune Würmer" erblickt habe, „die sehr ämsig waren, und ihre 6. langen Beine mit ungemeiner Geschwindigkeit zu gebrauchen wusten“. Er hielt „sie sogleich für das, was sie waren, nemlich für diejenige Art Blatlausfreßer, die bei dem Herrn von RÉAUMUR die zwote Claße machen, und welchen er den Nahmen Blatlaus-Löwen, Lion de Pucerons, gegeben hat“, womit VON GLEICHEN recht hatte. Er beschreibt die Larve von *D. phalaenoides* sehr genau und gibt eine gelungene Abbildung (Abb.11: Tab. III, Fig. 21-22). Erwähnung verdient auch seine Bemerkung über den Geruch der Larven, er sei „außerordentlich stark, und dabei sehr angenehm, nichts anders als Quändel und Thimian. Vielleicht ist er die Witterung der Blatläuse die sie locket, ihrem Feinde in der Nähe zu bleiben.“ Tatsächlich haben die Larven von *D. phalaenoides* einen charakteristischen Geruch, den FULMEK (1941) mit dem von Anis- oder Fenchelöl vergleicht. VON GLEICHEN beschreibt das Verhalten der Larven sehr treffend und widmet sich dann recht ausführlich den Mundwerkzeugen. Er lobt auch an dieser Stelle zunächst die Arbeiten von RÉAUMUR, schreibt aber dann, dass er – RÉAUMUR – „gleichwohl bei der Untersuchung erstgedachter Kopfteile des Blausfreßers [sic!], ohnfehlbar aus Mangel recht brauchbarer Vergrößerungswerkzeuge, dießmal von seiner gewöhnlichen Bahn abgekommen“ sei. Und weiter meint er, er habe daher „viel vergebliche Zeit und Mühe angewendet, auch hier [seine] Beobachtungen“ mit jenen von RÉAUMUR „zu vereinigen, ohne die Oefnungen an den Spitzen der Fresszangen des Blatlausfreßers zu finden“. Darauf zitiert er RÉAUMUR im Original, der völlig richtig Bau und Funktion der Saugzangen beschreibt. Merkwürdig, dass VON GLEICHEN bei der Beschreibung der Mundwerkzeuge von *Drepanepteryx phalaenoides* nicht auf seine 1764 veröffentlichte Untersuchung über den „Blatlausfreßer ... an einem Hanflblat“ und auf das Bezug nimmt, was er dort über RÉAUMURS Meinung über die „Fresszangen“ gesagt hat, nämlich, dass sie nicht zum Fressen,

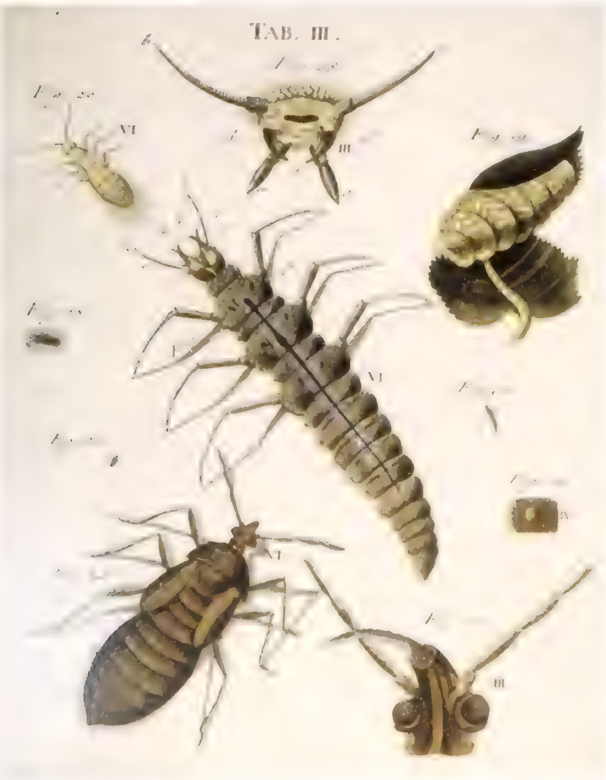


Abb. 11: W. F. VON GLEICHEN (1770), Tafel III. mit der Larve des „Ulmenblatlausfressers“ (= *Drepanepteryx phalaenoides*).

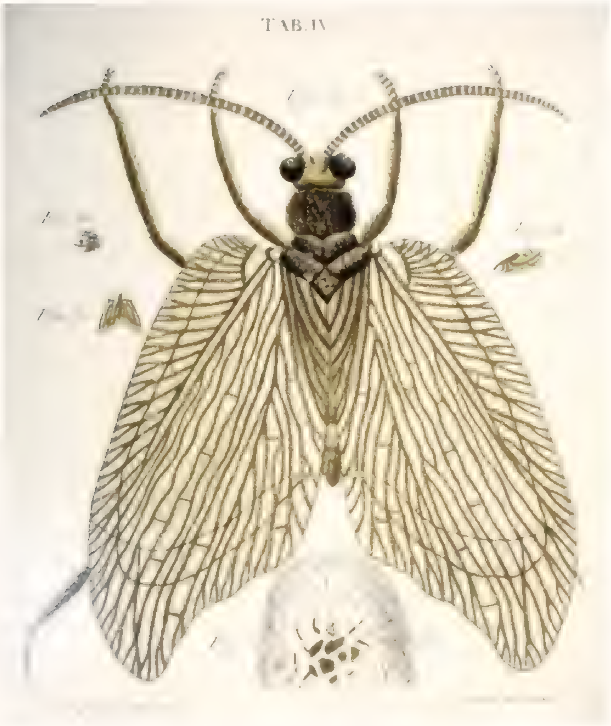


Abb. 12: W. F. VON GLEICHEN (1770), Tafel IV: mit Puppenkokon (Fig. 30) und Imago (Fig. 31-33).

sondern zum Saugen dienen und „hohl und an den Spitzen offen sind“ (siehe oben). Vielmehr kam er jetzt zu dem Schluss, dass sie an den Spitzen keine Öffnungen haben, weshalb er zwischen den Saugzangen nach der Mundöffnung suchte und schließlich eine solche auch fand und sogar abbildete (Abb.11: Tab. III, Fig. 23). Dazu schreibt er: „Da aber das Maul dieses Insekts nur alleine zum Saugen, und nicht zum Nagen gebrauchet wird, so ist auch der genaue Zusammenschlus der Lippen eine natürliche Folge dieser Bestimmung, so, wie der Unmöglichkeit, solches auf andere Art, als durch einen wohl angebrachten Druck des Kopfes zu öfnen und zu sehen.“ Die akribische präparative und mikroskopische Arbeit VON GLEICHENs verdient alle Bewunderung. Die Nahrung wird bei allen Neuropteren-Larven über die Saugzangen aufgenommen, die Mundöffnung ist eine zwischen den Saugzangen quer verlaufende, falzartig verschlossene, kaum erkennbare Spalte ohne jede Funktion für die Nahrungsaufnahme. Wie hat sich VON GLEICHEN die Nahrungsaufnahme wohl wirklich vorgestellt, da er meinte, das die „Fresszangen“ keine Öffnung haben, das Maul aber zum Saugen dient. Es ist tatsächlich erstaunlich, mit welcher Bestimmtheit VON GLEICHEN die richtige Deutung der Saugzangen durch RÉAUMUR verwirft und durch eine durchaus falsche und unlogische Behauptung ersetzt.

Dann beschreibt VON GLEICHEN die Entwicklung von *D. phalanoides*, gibt die Larvalperiode mit 13 bis 14 Tagen an, erwähnt den „Bemerkungswürdige[n] Umstand, bey diesem Insekt, daß es dieses mit den Spinnen gemein hat, aus dem Ende oder der Spize seines Leibes, und nicht, wie andere Insekten aus dem Munde zu spinnen, und zwar nur zu der Zeit, wenn man das Gespinnste zu seiner Verwandlung anfängt, ohne zuvor jemals nur das geringste Merkmal, daß er hiezu geschickt sey, gegeben zu haben.“ VON GLEICHEN gibt eine schöne Abbildung des Kokons (Abb. 12: Tab. IV, Fig. 30) und erwähnt dann, dass zwei Imagines geschlüpft seien. Es folgt eine ausführliche und anschauliche Beschreibung der Imago, ergänzt durch die schöne kolorierte Kupfertafel. Gerechterweise muss man aber sagen, dass die Art zwar sofort zu erkennen ist (nicht zuletzt, weil es in Europa keine andere nur halbwegs ähnliche Hemerobiiden-Spezies gibt und die zweite in Europa vorkommende Art des Genus, *D. algidus* (Erichson in Middendorf, 1851), sich habituell erheblich unterscheidet), dass aber das Geäder recht fehlerhaft gezeichnet ist. Auch hier gilt das bei VON GLEICHENs Abhandlung über die „Hofdame“ Gesagte. Im 18. Jahrhundert unterschätzte man einfach die Gesetzmäßigkeiten des Flügelgeäders von Insekten erheblich und achtete bei bildlichen Wiedergaben vielmehr darauf, den Habitus möglichst typisch zu erfassen – was VON GLEICHEN ja auch recht gut gelungen ist.

RÉAUMUR (1737) hat die Larve, den Kokon mit der Puppe und die Imago des 21 Jahre später von LINNAEUS

(1758) als *Hemerobius phalaenoides* gültig beschriebenen Insekts in Form sehr vereinfachter Zeichnungen dargestellt. Aber auch die nicht wenigen Abbildungen von *Drepanepteryx phalaenoides*, die nach VON GLEICHENs Monographie im 18. Jahrhundert erschienen, reichen qualitativ nicht annähernd an die (trotz des erwähnten Fehlers der Darstellung des Flügelgeäders) außergewöhnlich sorgfältig und vom Standpunkt der Ästhetik – damals und noch lange später – geradezu unerreichbaren Abbildungen des Schlossherrn von Greiffenstein heran.

GEUS (1989) bemerkt zu Recht, dass es unverständlich ist, dass die Arbeit VON GLEICHENs nicht nur unter dem Gesichtspunkt ihres aphidologischen, sondern auch unter jenem des neuropterologischen Inhalts vergessen oder ignoriert worden ist. Ganz stimmt dies aber doch nicht, weil sie von MORTON (1910) in seinem Aufsatz über die Biologie von *D. phalaenoides* ausführlich besprochen und von KILLINGTON (1936-1937) bei der Behandlung der Art erwähnt wurde.

5. SCHLUSSBETRACHTUNGEN

In der Geschichte der Neuropterologie nehmen VON GLEICHENs Arbeiten vor allem durch ihre prächtig kolorierte Kupferstiche mit den geradezu riesig dargestellten Insekten, die in allen drei Fällen eine Bestimmung der Spezies zulassen, einen besondern Platz ein. Seine sorgfältigen Beschreibungen von morphologischen Merkmalen, Entwicklung und Verhaltensweisen der von ihm untersuchten Neuropteren – *Chrysopa pallens* (Rambur), *Chrysoperla carnea* (Stephens) und *Drepanepteryx phalaenoides* (Linnaeus) – haben daher umso größeren Wert. Die meisten Abbildungen und Beschreibungen von Chrysopiden und Hemerobiiden durch frühere Autoren sind – von *D. phalaenoides* abgesehen – keinen wirklich identifizierbaren Spezies zuzuordnen. Dennoch muss man zugeben, dass VON GLEICHENs Arbeiten keine Erkenntnisse enthalten, die so grundlegend neu wären, dass sie die weitere neuropterologische Forschung entscheidend und nachhaltig beeinflusst hätten. Dies ist wohl der wichtigste Grund dafür, dass diese Publikationen fast oder sogar völlig in Vergessenheit geraten sind.

Ein anderer Grund mag darin zu finden sein, dass die Bücher VON GLEICHENs durch die vielen kolorierten Tafeln auch zur Zeit ihrer Veröffentlichung (und nicht nur heute) teuer und daher nur einem kleinen Kreis von Lesern zugänglich waren.

VON GLEICHEN hat alle drei neuropterologischen Arbeiten nach dem Jahr 1758 veröffentlicht. Hätte er die von ihm untersuchten Chrysopiden mit lateinischen Namen versehen, so hätten diese nomenklatorische Gültigkeit erlangt, und er wäre der Autor der in der gesamten entomologischen und insgesamt biologischen Literatur am häufigsten behandelten Neuropteren-Art geworden – oder auch nicht, da er ja der Meinung war, dass sein „Blatlausfreßer an einem Hanfblat“ und seine Hofdame ein und dieselbe Art darstellten. Dass er seinen „Ulmen-Blatlausfreßer“ nicht dem von LINNAEUS 1758 beschriebenen *Hemerobius phalaenoides* zugeordnet hat, ist erstaunlich.

VON GLEICHEN legte auf die Beschreibungen neuer Arten wahrscheinlich wirklich keinen Wert, doch muss man auch bedenken, dass ihm die Vorkenntnisse und wissenschaftliche Ausbildung fehlten. Es ist unwahrscheinlich, dass er die lateinische Sprache (in der die meisten entomologischen und jedenfalls alle systematischen Werke damals verfasst wurden) beherrschte, hingegen hat er mit Sicherheit fließend Französisch gesprochen, weil dies die Sprache der Aristokratie des 18. Jahrhunderts war. Das in französischer Sprache geschriebene Werk von René Antoine Ferchault de RÉAUMUR (1683-1757) hat er daher, nachdem es ihm zu Beginn der 60er Jahre in die Hände gekommen war, oft und gerne benützt, und er hat immer wieder seine Bewunderung für dieses Werk – das tatsächlich einen Meilenstein in der Geschichte der Entomologie darstellt – zum Ausdruck gebracht.

VON GLEICHEN muss tatsächlich nicht nur ein von wirklicher Neugierde, die Natur zu erforschen, durchdrungener, scharfsinniger und unerhört geduldiger Beobachter und Experimentator und hochbegabter Zeichner gewesen sein, sondern einfach ein ungewöhnlich intelligenter Mensch, so dass er es letztlich geschafft hat, einen Platz in der Geschichte der Naturwissenschaften zu erobern, obwohl er in seiner Kindheit nicht einmal eine handfeste Schulausbildung genossen hatte und erst jenseits des 40. Lebensjahrs begonnen hatte, sich für die Natur zu interessieren.

Dies erklärt auch die manchmal erstaunliche Einschätzung des Neuheitswerts seiner „Entdeckungen“ – ein Phänomen, das man auch heutzutage immer wieder finden kann. Eine schon in der Kindheit oder frühen Jugendzeit einsetzende Neugierde für die Natur (oder *mutatis mutandis* für irgendein anderes Gebiet) und eine solide und lange Ausbildung führen zunächst zur frühen Vertrautheit mit dem, was andere vorher erforscht und entdeckt haben und bewahren weitgehend vor der Meinung, dass alles, was man nicht selbst kennt, grundsätzlich unbekannt ist und eine neue Entdeckung darstellt. Unter diesem Gesichtspunkt ist manche überaus selbstsichere, unbekümmert anmutende Aussage, ist aber auch manche abfällige und geradezu hochmütig anmutende Feststellung VON GLEICHENs zu sehen. Die Kenntnis dessen, was andere schon längst oder erst kürzlich vor einem selbst gefunden haben, ist oder zumindest war bis vor kurzer Zeit – abgesehen von einer gründlichen Ausbildung – an eine umfangreiche Bibliothek oder zumindest an den Zugang zu einer solchen gebunden, heute kann das mehr und mehr durch den Zugang zu elektronischen Datenbanken ersetzt werden. Nicht ersetzbar sind indes die möglichst früh einsetzende Befassung mit den Objekten der Neugierde und eine intensive Ausbildung, die zwar praktischerweise durch Gymnasien und Universitäten vermittelt wird, aber – wie viele eindrucksvolle Beispiele der Wissenschaftsgeschichte und sogar das des „spät berufenen" Autodidakten Wilhelm Friedrich VON GLEICHEN zeigen – nicht notwendigerweise an diese Institutionen gebunden ist. VON GLEICHEN ist – als schon 43jähriger – bei Martin Frobenius LEDERMÜLLER (1719-1769) „in die Lehre gegangen", und er hat allmählich Kenntnis von den früheren Autoren erhalten. Dass er den von ihm so sehr verehrten und aufrichtig bewunderten R. A. F. DE RÉAUMUR voreilig und unbegründet kritisiert hat (siehe oben), ist bemerkenswert.

Wie immer auch: Wilhelm Friedrich VON GLEICHEN gebührt jedenfalls auch in der Geschichte der Neuropterologie ein markanter Platz – was mit der vorliegenden Studie gezeigt und bekräftigt werden sollte.

Widmung. Wir widmen diese Arbeit dem Andenken unseres Freundes Clas Naumann. Die Liebe zu den alten Büchern unserer Wissenschaft und das Interesse für die Geschichte der Entomologie haben wir mit ihm geteilt, und viele Gespräche mit ihm waren diesem Thema gewidmet. Noch zu Beginn des Jahres 2004 – wenige Wochen, bevor sein Leben zu Ende ging – haben zwei entomologisch-historische Bücher mehrere Telefongespräche geprägt. Zum einen befasste er sich zu Ende des Jahres 2003 mit einer Rezension des im Taschen-Verlag erschienenen und von einem Wissenschaftler-Team unter der Federführung von Prof. Dr. Rainer Willmann wissenschaftlich betreuten Prachtwerkes über die Tafeln der 1734-1765 erschienenen Rerum Naturalium Thesauri von Albertus Seba. Die Rezension (NAUMANN 2003a) erschien im Dezember 2003; er schickte uns noch ein Exemplar des Hefts der Entomologischen Zeitschrift mit persönlicher Widmung, es sollte die letzte Arbeit sein, die wir von ihm bekommen haben, und – zusammen mit dem, im selben Heft veröffentlichten spannend zu lesenden Aufsatz über „Die höchste Zygaene der Welt" (NAUMANN 2003b) wohl auch die letzte seiner Publikationen, die zu seinen Lebzeiten erschienen ist.

Zum zweiten erzählte er in den ersten Januartagen 2004 einem von uns (H.A.) von einem besonderen Geschenk, das er zu Weihnachten bekommen habe: ein eben erschienenes Buch über die Augsburger Naturforscher des 18. u. 19. Jhdts. Dieses Buch (PFEUFFER 2003) hat ihm in seinen letzten Lebenswochen tiefe Freude gegeben. Wir haben es sogleich erworben und auch noch mit ihm darüber gesprochen; es ist tatsächlich für jeden, dem die Namen Jacob HÜBNER, Gottlieb Tobias WILHELM und Christian Friedrich FREYER etwas sagen, ein intellektueller Genuss ersten Ranges.

Wir haben Clas NAUMANN erstmals im März 1964 bei der Entomologen-Tagung in München getroffen, wir kannten ihn also genau 40 Jahre. Viele gemeinsame Interessen haben zu vielen Begegnungen und vielen substantiellen Gesprächen geführt, in denen wir immer wieder seine hohe Intelligenz, seine schier unerschöpfliche Arbeitskraft, seine unnachgiebig kompromisslose Einstellung zur Mittelmäßigkeit in der Wissenschaft, seine außerordentliche Hilfsbereitschaft und seinen unglaublichen Einsatz für die, die seiner Hilfe bedurften, bewundern konnten. Wir sind dankbar für die lange Zeit unserer Freundschaft mit ihm, und wir danken ihm für die intellektuelle und menschliche Bereicherung, die wir durch ihn erfahren haben.

Danksagung. Unser besonderer Dank gilt Herrn Prof. Dr. Peter Duelli (Eidgenössische Forschungsanstalt WSL, Birmensdorf, Schweiz) für seine Beurteilungen der Abbildungen in den beiden Arbeiten VON GLEICHENs, die sich mit Chrysopiden befassen. Prof. Duelli ist einer der international führenden Experten sowohl für präimaginale Stadien von Chrysopiden generell als auch für das Genus *Chrysoperla*, dessen Arten und song-morphs. Herrn Dr. Hieronymus Dastych (Zoologisches Institut und Zoologisches Museum der Universität Hamburg) danken wir für die Überlassung eines Originals der Arbeit von H. WEIDNER (1980).

6. ZUSAMMENFASSUNG

W. F. VON GLEICHEN, ein fränkischer Edelmann, der nach einer erfolgreichen Militärlaufbahn und einem luxuriösen Hofleben erst um sein 40. Lebensjahr seine Leidenschaft für die Erforschung der Natur entdeckte und sich fortan mit vielen verschiedenen zoologischen, botanischen, landwirtschaftlichen und technischen Fragen beschäftigte und ab 1757 regelmäßig über seine Forschungen publizierte, wurde schließlich einer der herausragenden deutschen Mikroskopiker der 2. Hälfte des 18. Jahrhunderts. Er verfasste auch drei Arbeiten, die drei verschiedenen Neuropteren-Arten gewidmet waren. Alle drei Publikationen sind mit sehr schön kolorierten Kupferstichen ausgestattet, die Darstellungen und Beschreibungen sind so gut und jedenfalls ausreichend, um in allen Fällen eine Artbestimmung zuzulassen. VON GLEICHEN hat die von ihm untersuchten Insekten nicht mit nomenklatorisch gültigen Namen versehen, sondern ihnen deutsche Namen gegeben.

Die erste Arbeit (1764) behandelt die gestielten Eier, den Schlüpfvorgang und die morphologischen Merkmale der Erstlarve des 74 Jahre später von RAMBUR (1838) beschriebenen *Hemerobius pallens*, heute *Chrysopa pallens* (Chrysopidae).

Die zweite Arbeit (1764) ist der Beschreibung einer im Winter im Zimmer gefundenen bräunlichen Florfliege gewidmet. Es handelt sich dabei um jene Art, die STE-

PHENS (1836), also 72 Jahre später als *Chrysopa carnea*, heute *Chrysoperla carnea*, beschrieben hat. *Ch. carnea* ist mit Abstand die am besten untersuchte und in unzähligen Publikationen behandelte Neuropteren-Art.

Die Abbildung dieser Art durch VON GLEICHEN in Form eines kolorierten Kupferstiches ist wahrscheinlich die älteste bis zur Art identifizierbare Darstellung einer Florfliege und zugleich die größte jemals publizierte Illustration einer Chrysopidae.

Die dritte Arbeit ist 1770 und in einer zweiten Auflage 1787 als kleine Monographie der Ulmenblattlaus (*Brysocyrpta ulmi* [Linnaeus,1758]) erschienen; in ihr werden auch der 12 Jahre vorher von LINNAEUS (1758) als *Hemerobius phalaenoides* beschriebene Prädator *Drepanepteryx phalaenoides* (Hemerobiidae) unter morphologischen, biologischen und ethologischen Gesichtspunkten ausführlich beschrieben und als Larve und Imago in Form kolorierter Kupferstiche abgebildet, auch diese Illustrationen fallen durch ihre Größe aus dem Rahmen. Über diese Arbeit VON GLEICHENs gibt es wegen ihres bedeutenden aphidiologischen Inhalts Sekundärliteratur, die beiden ersten Artikel scheinen allerdings völlig in Vergessenheit geraten zu sein.

7. SUMMARY

W. F. VON GLEICHEN, a Franconian nobleman, discovered his deep interest and ardour for exploring nature around his 40th year of life – after a successful military career and luxurious life at various courts. From that time onwards he spent a lot of time with various zoological, botanical, agricultural and technical questions, published regularly on results of his research work and became one of the outstanding German microscopists of the second half of the 18th century. Among his publications, there are also three, each dealing with a certain species of Neuroptera, which impress also because of the brilliant hand-coloured copper plates. The descriptions and illustrations are of a quality which allows an identification of the species.

The first paper (1764) deals with the stalked eggs, hatching and morphological characters of the first instar larva of that species of Chrysopidae (Green lace-wings) which was described by RAMBUR (1838) as *Hemerobius pallens*, today *Chrysopa pallens*. This is the oldest illustration of a larva of a species of the family Chrysopidae which can be identified on the species level.

The second paper (also published in 1764) deals with a reddish – brownish lacewing which was on the wings in a warm room in January. The illustrations and the circumstances of the finding clearly allow to identify the species as that one which STEPHENS (1836), 72 years later, described as *Chrysopa* (today: *Chrysoperla*) *carnea*. *Ch. carnea* is by far the most intensively studied lacewing, and countless publications deal with it. VON GLEICHEN's illustration is the first one of a Chrysopid in the whole literature which allows the definite identification of the species figured. Moreover, the illustration is apparently the largest figure of a neuropteroid insect ever published.

The third publication (which appeared first in 1770 and in a second edition in 1787) is a small monograph on the elm aphid (*Brysocrypta ulmi* [Linnaeus 1758]), which also deals with a predator of the aphid, a neuropteroid species described by LINNAEUS (1758) as *Hemerobius* (today: *Drepanepteryx*) *phalaenoides*. Larva, cocoon with the pupae, and the adult are described from a morphological, biological, and ethological view. The larva and the imago are beautifully figured. Again, these illustrations are of an unusual large size in the whole neuropterological literature. This monograph by VON GLEICHEN has been cited and even treated in the later literature, mainly for its aphidiological contents on several occasions, the two other articles have, however, been forgotten entirely.

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Bonner zoologische Beiträge | Band 53 (2004) | Heft 1/2 | Seiten 27–36 | Bonn, Juni 2005

On the Biology of the Ivy-Bee *Colletes hederae* Schmidt & Westrich, 1993 (Hymenoptera, Apidae)[1]

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Abstract. The biology of *Colletes hederae* Schmidt & Westrich, 1993, a bee species oligolectic on ivy (*Hedera helix*), was studied in late summer 2003 at a nesting aggregation in Dirmstein near Grünstadt (Pfalz), Germany. We analysed the diurnal foraging rhythm, pollen carrying capacity, rate of reproduction, nest architecture, requirements on the nesting habitat and dependence on climatic parameters. In addition, the distribution of *C. hederae* is revised and represents an adriato-mediterranean distribution type. All known localities of this species fall within the distributional area of *Hedera helix*. *Colletes hederae* seems to prefer inclined and southward exposed nest sites in sand or loess soils. The females of *C. hederae* started their first trip on average at 9.52 h in the morning, made 5.5 provisioning trips and returned from their last trip at 17.09 h. The mean duration of all provisioning trips was 60 minutes but the first flight in the morning was significantly longer (90 min) than the subsequent trips of the day. This is interpreted as additional adult feeding on nectar after a night in the nest. The duration of provisioning trips decreased with increasing temperature. The oligolecty of *C. hederae* was confirmed. *Colletes hederae* collected on average 0.5 million grains per pollen load and the cells contained 2.8 million grains. Four nests were excavated; the main burrow ran between 7 and 12 cm horizontally into the steep face and the first cells occurred at a depth of 30-45 cm. Beyond a depth of 60 cm no cells were found. Between four and eight cells branched off the vertical part of the main burrow; side burrows were only found in one nest. During the extraordinarily warm and dry season of 2003, the females completed up to 18 cells.

Key words. Distribution, diurnal foraging rhythm, pollen carrying capacity, reproduction rate, nest architecture

1. INTRODUCTION

Colletes hederae was described as a new species only in 1993 (SCHMIDT & WESTRICH 1993), based on specimens collected in Germany and Croatia (Fig. 2). The species appears to be uncommon and is known from few localities. This species is also recently recorded from Great Britain, Luxembourg, The Netherlands, Belgium and Spain (FEITZ 2001, PEETERS et al. 1999, PETIT 1996, RATHJEN 1998). *Colletes hederae* was probably recognized as a distinct species so recently because all species of *Colletes* are morphologically very similar and it particularly resembles *C. succinctus* (Linnaeus) and *C. halophilus* Verhoeff. Furthermore, *C. hederae* is active in autumn when most other bees have finished their life cycle and ivy was not considered as an attractive pollen source for bees before.

In the past 20 years important new data on the biology of bees were gathered and published. In Germany, Paul WESTRICH (1989) set the standard for many other subsequent books dealing with the biology of bees (BELLMANN 1995, SCHMID-EGGER et al. 1995, MÜLLER et al. 1997). Taking a more global view, "The bees of the World" by Charles D. MICHENER (2000) set a milestone in the history of literature on bees at the beginning of the millennium. Nevertheless, exact data on the biology of many of the more than 16,000 species worldwide or about the 550 German species of solitary bees are scarce or not available. Likewise, the biology of the newly described *Colletes hederae* is largely unknown. Biological data are needed to support taxonomic decisions as in the case of *C. hederae*, *C. halophilus* and *C. succinctus*, but also to understand the mechanisms of speciation. Lastly, good knowledge of the biology and habitat requirements of the species facilitates conservation measures.

The aim of the present study was therefore to investigate the biology of *Colletes hederae* including the diurnal foraging rhythm, pollen carrying capacity, rate of reproduction, nest architecture, requirements on the nesting habitat and dependence on climatic parameters. Furthermore the current distribution of the species is reviewed.

2. MATERIALS AND METHODS

2.1. Study area

The study area is located in southwestern Germany near the city of Grünstadt (Pfalz) in a village called Dirmstein (49°34'04''N, 08°14'22''E). The nest aggregation of *C. hederae* was discovered in 1994 (NIEHUIS pers. comm. Bonn 2003, SCHMID-EGGER 1997) and is situated on a steep face of loess below a vineyard. The steep face has a total length of approximately 150 m and is exposed southwards. The climate is sub-oceanic with mild winters, a summer maximum of precipitation (59-71 mm per m^2 and year) and an annual mean temperature of 10.2° C.

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[1] In commemoration of Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004)

2.2. Abiotic parameters

Climatic parameters were measured with data loggers (Orion Tiny Logger Manager OTLM Tinytalk©). The soil temperature was taken half-hourly at a 20 cm depth on the steep face, air temperature and atmospheric humidity were recorded every quarter of an hour in a portable weather station at a height of 2 m. Data of the "Deutscher Wetterdienst – Station Mannheim" were also used. The soil type was characterized using a soil particle size analysis and we determined the soil density. Furthermore we calculated the inclination of the steep face. The host plant *Hedera helix* LINNAEUS was mapped in a radius of 500 m around the nesting aggregation.

2.3. Ethological observations

We observed the behaviour of 16 different females for five days during September 2003. Marking tests at the beginning of the season showed that the females were very sensitive to this interference (cf. BISCHOFF et al. 2003) and consequently we decided to mark only the nests of the respective females. Nests were marked with coloured toothpicks. We recorded the time of first departure, number of foraging trips, last return and digging activity. A total of 168 data sets were documented. Since the activity of most bees is extremely influenced by weather conditions (BISCHOFF et al. 2003, LARSSON 1991, LIND 1968) we created a measure for the bees' activity independent from weather conditions (cf. MÜLLER 1994) which is referred to as a so-called "bee-day"(BD). One bee-day corresponds to a day with optimal weather conditions, which females could use completely for provisioning activities. The observed flying activity on days with optimal conditions was 8 hours. The mean temperature at those optimal days amounted to 17°C and the duration of sunshine was between 8 and 10 hours.

2.4. Pollen analysis

For pollen analysis, 15 females of *C. hederae* were captured and transferred in vials with 70% ethanol. To remove the complete pollen load from the bees, all body parts (legs and sometimes thorax without wings) were sonicated in vials filled with a liquid medium (cf. BUCHMANN & SHIPMAN 1990). Furthermore we excavated 20 cells of *C. hederae*, removed the cell lining, larva and stored the pollen load in ethanol. The number of grains per pollen load or cell was determined using an electronic particle counter (Casy© cell counter and Analyser). To calculate the mean number of pollen grains per pollen load and cell, only particles between 20 and 30 µm were considered since they represent the grain size of *Hedera helix*. All pollen load and cell samples were qualitatively checked with a scanning electron microscope. The pollen samples were treated with Diethylether to remove pollen cement and with 1,1,1,3,3,3,-Hexamethyldisilazam to avoid deflation.

2.5. Nest excavations

Only nests with observed female activity were excavated at the end of the season. Due to the high inclination, nests could not be poured out with plaster. We excavated the nests by following the main burrow from the nest entrance and removed with a spoon the soil layers very carefully until the first cell appeared.

3. RESULTS

3.1. Abiotic characteristics

The observed nesting aggregation extended over a breadth of 8 m of the steep face. The height of the steep face amounted to 8.65 m at the studied aggregation. The base of the steep face ran with an inclination of 130° up to a height of 2.65 m and above this height the angle was nearly 90°. At a height of 2 m a line of natural grass cover could be identified and a total of 30% of the studied aggregation was covered with vegetation.

The mean values of air temperature, soil temperature, humidity and hours of sunshine at the study area (onsite measurements) and from the nearest weather station are documented in Table 1. No significant differences between our data and the data of the local weather station at Mannheim were found.

Table 1: Mean climatic parameters measured during five field days in September 2004 (DWD = local weather station at Mannheim)

	Air temp. (°C)	Soil temp. (°C)	Humidity	Hours of sunshine
On-site data	22.76 ± 4.42	21.48 ± 2.70	39.53 ± 11.90	
DWD	21.70 ± 3.58		39.38 ± 11.88	9.71 ± 1.06

The mean soil density amounted to 1.18 g/cm³ (n = 6) and the grain size analysis revealed a typical loess soil comprising 78% silt, 15% clay and 7% sand.

3.2. Distribution of *C. hederae*

Colletes hederae has been recorded from the following localities in nine countries of southern and western Europe (Fig. 1):

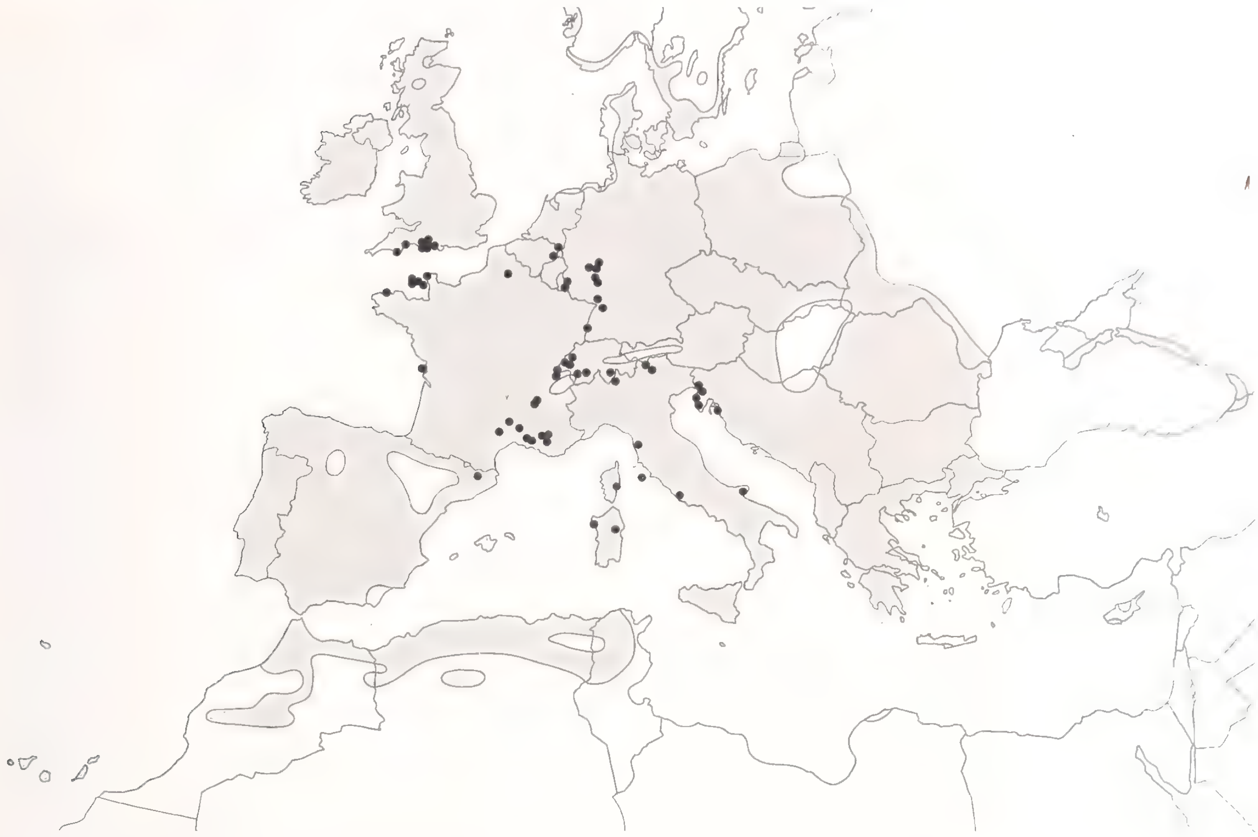

Fig. 1: Distribution area of *Hedera* (shaded) (after MEUSEL 1978) and records of *Colletes hederae*.

Belgium: Bassenge (PETIT 1996); **Croatia:** Lopar: Francelici/Matahlici, Rovinj: 2 localities; **France:** Ile-de´Oléron, Le Caylar, St. Chaptes, St. Jean-du-Gard (SCHMIDT & WESTRICH 1993), Bathernay, Buoux: Le Fort, Fontvieille, Lacoste, Maussane-les-Alpilles, Paradou, Pargny, Ratières, Rempoul: near St. Pol, Rustrel (WIERING 1999), Cherbourg Peninsula: north coast (EDWARDS & TELFER 2001), Avelmes, Corse: Caleraggio; **Germany:** Karlsruhe-Durlach (SCHMIDT & WESTRICH 1993), Alsheim, Bockenheim, Dirmstein, Flörsheim, Jockgrim, Monsheim, Nackenheim, Oppenheim (SCHMID-EGGER et al. 1995), Oestrich-Winkel (TISCHENDORF 1997), Burkheim (WESTRICH & DATHE 1997), Ihringen (SCHWENNINGER, pers. com.); **Great Britain:** Guernsey (Channel Island): 38 localities (SCHMIDT & WESTRICH 1993, EDWARDS & TELFER 2001, BWARS data base), East Prawle, Isle of Portland, Lulworth: 3 localities, Ringstead Bay, Swanage: 6 localities, Weymouth, Worth Matravers: 3 localities (CROSS 2002, BWARS data base), Branscombe, Corfe Castle, Herm (Channel Island), Jersey (Channel Island), Kimmeridge, Langton Matravers, Lihou (Channel Island), Osmington Mills, Preston Winslow, Sark (Channel Island): 4 localities, Ulwell: Godlingston Hill, Wareham, Wool, (BWARS data base); **Italy:** Bolzano, Isola del Gilio, Merano (SCHMIDT & WESTRICH 1993), Lazio: Albano (WIERING 1999), Calci, Mte. Gargano: M.S. Angelo, Sardinia: Alghero, Sardinia: Oliena, Varenna; **Luxembourg:** Remerschen, Schwebsange, Stadtbredimus, Wintrange (FEITZ 2001); Netherlands: Maastricht, Botanical Garden Lichtenberg (LEFEBER 1998); **Slovenia:** Kras: Brje pri Komnu, Kras: Gorjansko (GOGALA 1991), Hrastovlje (GOGALA 1994); **Spain:** Girona: Les Preses (RATHJEN 1998); **Switzerland:** Biasca: near river Brenno, Châble-Perron: Cheseaux, Lalden: banks of river Rhone near Taleia, Peney, Russin: 2 localities, Sion, Yverdon-les-Bains (AMIET et al. 1999, CSCF data base), Les Bioux: Lac de Joux (AMIET pers. com.).

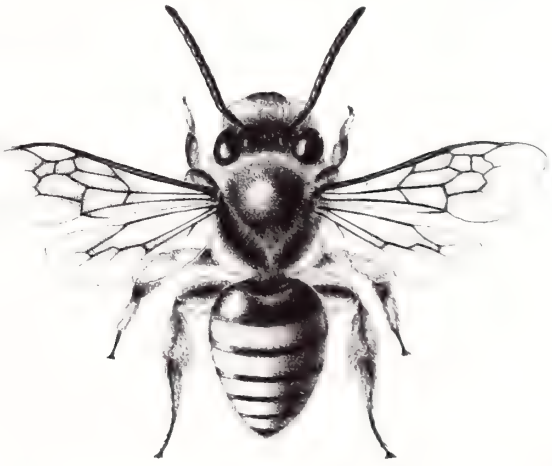

Fig. 2: *Colletes hederae* male (drawing by Florian Thümmel).

The distribution of *C. hederae* extends from central Italy, Sardinia and northeast Spain in the south, to southwest Germany, Netherlands and the southern parts of Great Britain in the north. The east-west range is from Slovenia to the English Channel. On the whole *C. hederae* represents an adriato-mediterranean distribution type (LATTIN 1967). All known localities of this species fall within the distribution of *Hedera helix* but its range is much smaller than that of its host plant (Fig. 1). *Hedera helix* occurs from North Africa in the south to southern Scandinavia in the north and from the Canaries and United Kingdom in the west eastwards to the coast of the Black Sea (MEUSEL 1978).

3.3. General behaviour of males and females

The first males patrolling at the aggregation were observed on the 24th of August. The males often interrupted their searching flights with inspections of the nest entrances of the previous years. The first flight was repeatedly preceded by grooming at a nest entrance. On the subsequent days the males appeared successively earlier in the morning at the aggregation, e.g. on the 1st of September the first male was recorded at 8.30 h. An obvious correlation between male activity and sunshine was observed. When the sun disappeared, the activity of the males stopped immediately and recurred directly when the sun came out again.

The first females were discovered on the 1st of September, but it was a matter of only a few individuals and the ivy was not yet in bloom. Only five days later, on the 6th of September, several hundred females were recognised. An emerging female was pounced upon at once by several males trying to mate and they formed a characteristic copulation cluster. The copulation cluster frequently tumbled down to the base of the steep face where mating with one male took place. Females that had already mated were mostly ignored by patrolling males. This behaviour could be observed directly after copulation. The phase of copulation lasted only from the 6th to 10th of September.

Shortly after having mated the females started to dig and provision a nest. Many females apparently chose old nests and expanded the old burrows. Other females favoured to dig a new nest, mainly at places that were hidden behind grass or other vegetation. Traces of digging activity could be observed sometimes in the morning at the nest entrances, which meant that the females continued with nest construction after their last foraging trip on the previous day. The females did not close the nest entrance after leaving. Usually they found the entrance immediately when they returned from a provisioning trip. However, changes to the last detail (e.g. marking with a toothpick) were followed by orientation flights in the shape of increasing zigzag flights. If the next approach was not successive, the females rested in the surrounding area and searched on the ground with their antennae, or rested on neighbouring vegetation and started a new approach after a few minutes. None of the observed females constructed a second nest at the observed aggregation. No parasites were observed at the aggregation.

3.4. Diurnal foraging rhythm and reproduction

The females started their first trip at 9.52 h in the morning, after waiting and trilling with their antennae a few minutes at the nest entrance. The earliest observed flight started at 09.07 h and the latest at 12.19 h. On average *C. hederae* made 5.5 provisioning trips and returned from its last trip at 17.09 h. The earliest return was at 16.19 h and the latest at 17.53 h (Fig. 3). The mean du-

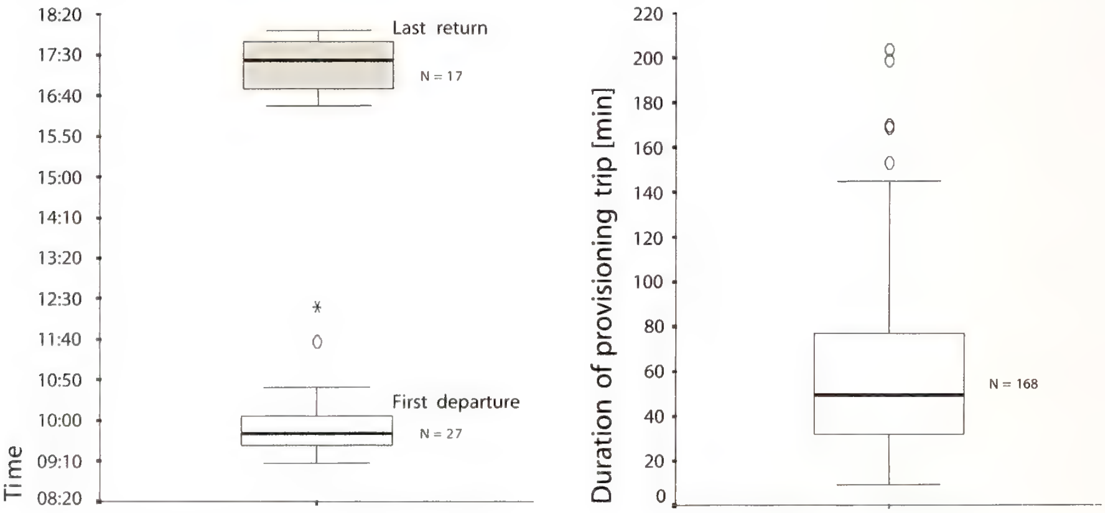

Fig 3: Time range of main activity data as the departure for the first trip, the last return to the nest and the duration of provisioning flights.

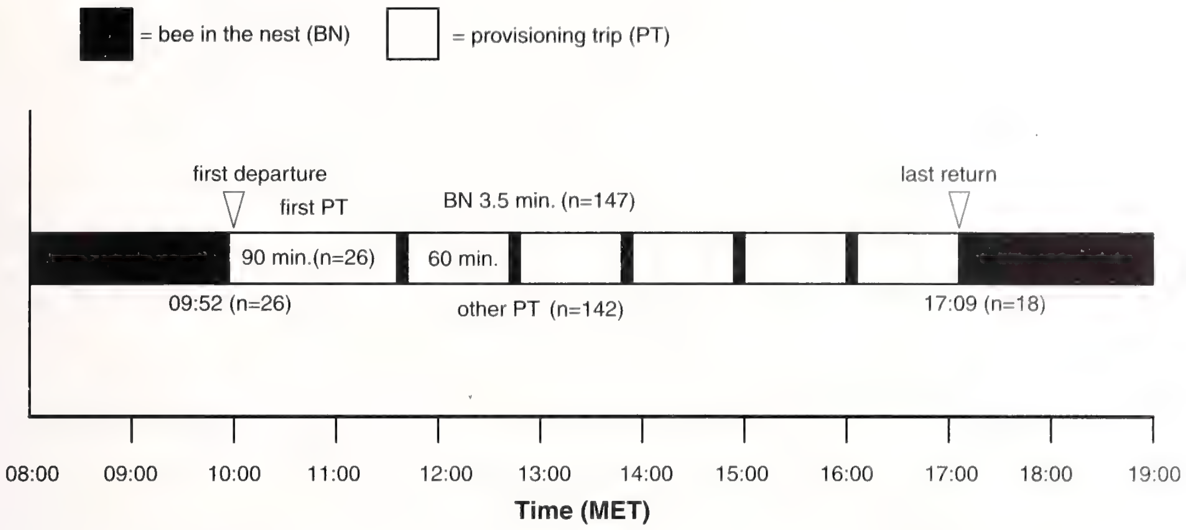
= bee in the nest (BN)
= provisioning trip (PT)
first departure
first PT
BN 3.5 min. (n=147)
last return
90 min.(n=26)
60 min.
09:52 (n=26)
other PT (n=142)
17:09 (n=18)
08:00
09:00
10:00
11:00
12:00
13:00
14:00
15:00
16:00
17:00
18:00
19:00
Time (MET)

Fig. 4: Ethogram of an average daily foraging cycle of *C. hederae.*

ration of all provisioning trips was 60.3 ± 39.9 min (n = 169). However, the first flight in the morning was significantly longer (90 min) than the other trips of the day (Wilcoxon-test: Z = -2.767, p = 0.006, n = 16). The activity in the nest after one provisioning trip amounted to 3.5 ± 1.7 min (n = 165). No significant correlation between the activity in the nest and the preceding provisioning trip could be detected. A scheme of the average foraging behaviour of *C. hederae* is documented in an ethogramm (Fig. 4).

The estimation of the time that the bees used for provisioning behaviour independent of weather conditions revealed 12 complete and 12 half = 18 BDs. Assuming five provisioning trips for one cell (see below), *C. hederae* could approximately complete between 12 and 18 cells during the season of 2003.

3.5. Dependence on climatic parameters

We correlated the different activity data (departures, length of provisioning trips and nest activity) with climatic parameters. The results are presented in Table 2. A highly significant negative correlation between the duration of provisioning trips and temperature was found: the higher the temperature, the shorter the provisioning trip (Fig. 5). The correlation between the time of first departure and temperature represents only the increasing number of starting bees with time, parallel to the increasing temperature and humidity with time.

Table 2 : Correlation of activity data with climatic parameters (pt = provisioning trip)

	Temperature (2m)	**Soil temperature**	**Humidity**
Duration of pt			
n	99	99	99
r	-0.290	0.089	0.155
p	0.004*	0.379	0.126
Time in nest			
n	146	146	146
r	0.101	0.001	-0.167
p	0.223	0.986	0.044*
Time of 1st trip			
n	26	26	27
r	-0.783	-0.042	-0.894
p	<0.001*	0.492	<0.001*

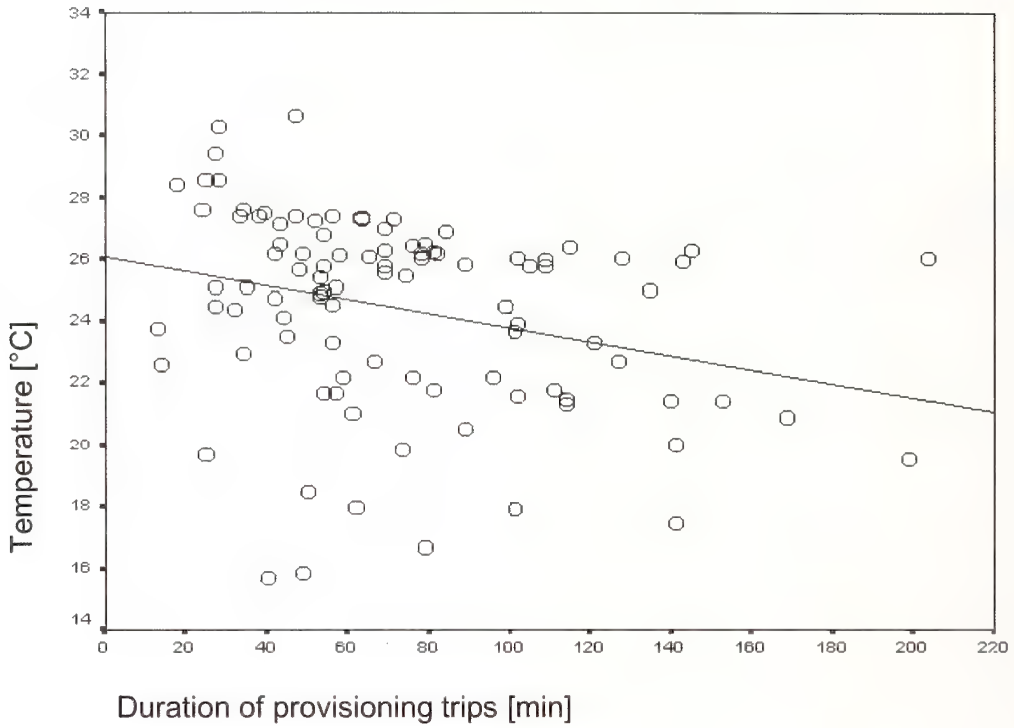

Fig. 5: Correlation (Pearson) between the duration of foraging trips and temperature.

3.6. Pollen

In all pollen loads and cells only pollen of *Hedera helix* (Fig. 6) was found. The mean longitudinal diameter of the pollen grains measured 38 ± 1.3 µm (n = 20), the equatorial diameter was 23 ± 1.3 µm (n = 20).

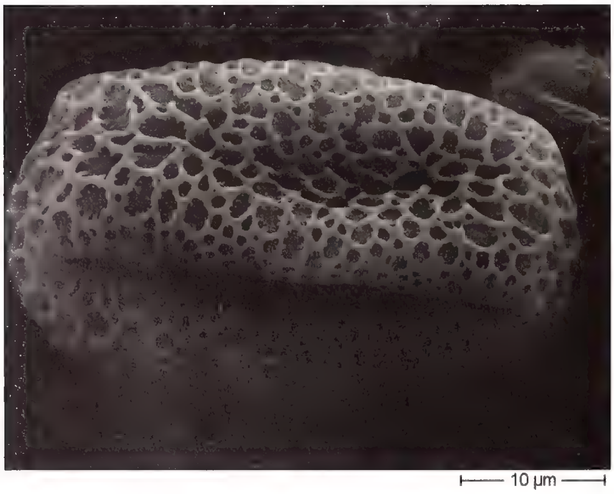

Fig. 6: SEM-Photograph of a pollen grain of *Hedera helix*.

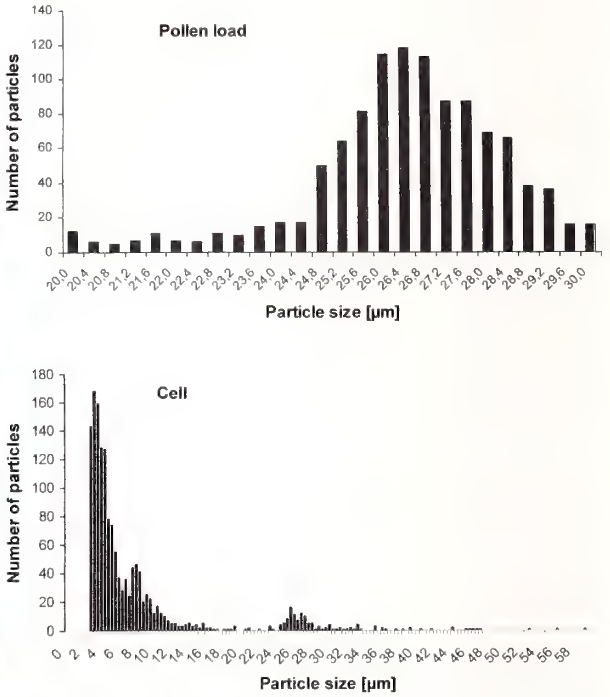

Fig. 7: Grain size distribution of one pollen load (only particles between 20 and 30 µm) and one cell (all particles) of *C. hederae* counted with an electronic particle counter in a volume of 1100 µl.

Colletes hederae collected on average 518103 ± 346639 (n = 15) grains per pollen load and the cells contained 2811816 ± 1843170 (n = 20) grains. Thus, the females had to make approximately 4 or 5 (5.4) provisioning trips to complete one cell. The grain size distribution of one pollen load and cell is documented in Figure 7.

3.7. Nest density and architecture

Most nests were found on sunny parts of the steep face, often covered by small tufts of grass. At the vertical part of the steep face more nests were located than at the base. Most females dug their nests above a level of 1 m. The mean number of nests was as high as 20 nests per m² in areas of the aggregation without vegetation cover, and up to 300 nests per m² in areas covered with grass.

We excavated four nests and the architecture is shown in Figure 8. In all four nests the main burrow first ran between 7 and 12 cm horizontally into the steep face. The first cells occurred at a depth of 30-45 cm and beyond a depth of 60 cm no cells were found. Between four and six cells were attached to one nest but presumably the number is higher. All cells branched off the vertical part of the main burrow. Only one of the four nests exhibited side burrows. The most conspicuous character of the architecture was the successive arrangement of cells (up to 4 cells) without side burrows.

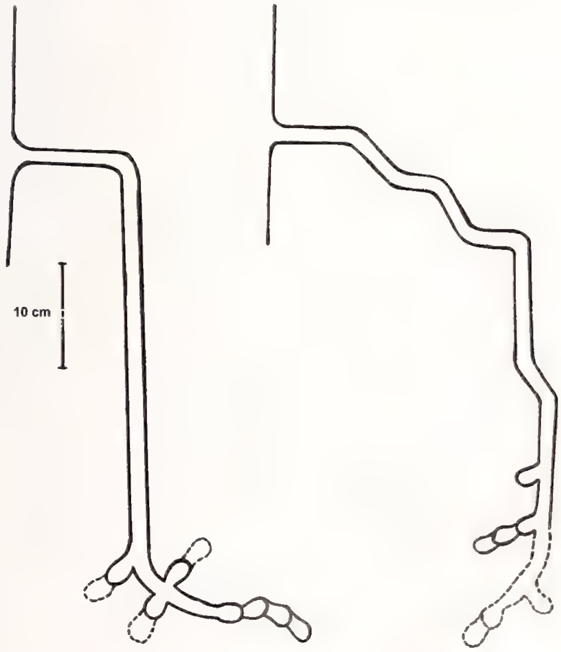

Fig. 8: Nest architecture reconstructed from four excavated nests of *C. hederae*.

The cell size measured on average 1-1.5 cm long with a diameter of 0.5 cm. The cells showed a convex shape at the side orientated to the main burrow and the membrane projected the cell at that end which optimised the successive arrangement of the cells. The fluid mixture of nectar and pollen filled approximately 2/3^{rds} of the cell.

4. DISCUSSION

4.1. Distribution

The distribution pattern of *C. hederae* can be interpreted as the result of the postglacial recolonization of parts of Europe from an Italian refuge (DE LATTIN 1967, HEWITT 1999). Its restricted distribution compared with the host plant may indicate a relatively recent origin of this species. The latter view is supported by the weak morphological differentiation of *C. hederae* and its assumed closest relatives.

Numerous *Colletes* species are oligolectic and collect pollen on the flowers of only one plant family or even a genus (MÜLLER & KUHLMANN 2003). Among them *C. hederae*, a member of the transpalaearctic *C. succinctus* species group (sensu NOSKIEWICZ 1936) that comprises 12 taxa, is unique because it is the only known bee species that is a specialised visitor of ivy (*Hedera helix*) (SCHMIDT & WESTRICH 1993). Species of the *C. succinctus* group show a close morphological resemblance and are often hard to identify. The phylogeny of the species within this group is not yet clear but there is some evidence that *C. succinctus* and *C. halophilus* are the closest relatives of *C. hederae*. Despite their close relationship, the flower visiting behaviour of the three species differs significantly. As far as known this is a unique case at least among the Old World *Colletes* and of special interest with respect to the understanding of evolution of oligolecty and speciation within the genus (KUHLMANN 2003). *Colletes halophilus* is a narrow endemic of costal sites of the southern North Sea and English Channel and an oligolege of Asteraceae. *Colletes succinctus* is widespread in the western Palaearctic and known to be an oligolege of *Calluna vulgaris* and *Erica* spp. (Ericaceae) (WESTRICH 1989), but in some populations of the British Isles exclusive pollen collecting on Asteraceae is documented (PERKINS 1945, EDWARDS & TELFER 2001). Phenology of all three species is similar, a single flight period in late summer / early autumn.

4.2. Pollen

The oligolecty of *C. hederae* was confirmed in this study. All 15 pollen loads and 20 cells contained only pollen of *Hedera helix*. The amount of grains per pollen load can only be compared with other species of the same genus since the pollen collecting apparatus varies much between different genera (BRAUÉ 1916; FRIESE 1923; GRINFELD 1962; PASTEELS & PASTEELS 1979) and such studies are rare. The only *Colletes* species for which such data are available is *C. cunicularius* (Linnaeus) (cf. BISCHOFF et al. 2003). *Colletes cunicularius* collects on average three times as much grains per load as *C. hederae*, but the latter species is much smaller than *C. cunicularius*. Furthermore these authors did not consider the percentage of particles out of the range of pollen grains, which must be subtracted. In the present study this percentage of "pollution" amounted to 60% even in the pollen loads. Furthermore the number of collected grains strongly depends on the grain size (SILVEIRA 1991; BISCHOFF et al. 2003). The grains of *Hedera helix* display approximately the same elliptical shape but are nearly twice as large as *Salix* grains. Only with volumetric calculations a comparison of the carrying capacity can be achieved. Therefore quantitative analyses of related species (which have the same size) and a volumetric comparison should be done.

4.3. Nest site selection and nest architecture

Like other *Colletes* species, *C. hederae* seems to prefer inclined and southward exposed nesting sites in sand or loess soils (cf. BISCHOFF 2000; MADER 1999). Likewise as with other congenerics *C. hederae* forms large aggregations. The nest architecture resembles that of *C. cunicularius* insofar as the short part of the horizontal main burrow is followed by a longer nearly completely vertical part and no real side burrows (K. FELTGEN pers. comm. Bonn 1997; MALYSHEV 1936). Nevertheless these authors did not mention a successive arrangement of several cells without side burrows. Only FRIESE (1923) figured a nest of *C. cunicularius* in which the cells were arranged successively. The successive arrangement of cells is also documented for *C. daviesanus* (Smith) (TISCHLER 1951; HAESELER 1972; MADER 1981; WESTRICH 1989). A comparison with the nest architecture of *C. halophilus* and *C. succinctus*, which remains to be discovered, would be interesting.

4.4. Diurnal and seasonal rhythm and reproduction rate

Seasonally overlapping bee species living in the same habitat often differ in their diurnal foraging rhythm (LEVERMANN et al. 2000; BISCHOFF et al. 2003). *Colletes hederae* is active in late summer and autumn when interspecific competition is reduced. This may have been one reason for a host switch to a late flowering host plant. The diurnal rhythm of *C. hederae* allows an optimal use of days with good flying conditions. One apparent character of the life cycle of *C. hederae* is the beginning of female provisioning behaviour shortly after mating without a resting period for oocyte maturation as reported in other species (cf. GEBHARDT & RÖHR 1987; MÜNSTER-SWENDSEN 1968; BISCHOFF 2001). *Colletes hederae* made five provisioning trips on average per day but on days with optimal weather conditions we observed several females that made up to 10 trips and were active eight hours of the day. *Colletes cunicularius*, a vernal species, makes on average seven trips per day and shows also flying activity between 8-9 hours on days with good flying conditions (BISCHOFF et al. 2003). Comparable to vernal species, autumnal species have to deal often with long periods of unfavourable weather conditions. Unlike the vernal *C. cunicularius*, *C. hederae* started its provisioning activity at a temperature threshold of 14.5 °C. This value is between the values of vernal and summer species and is also dependent of size (BATRA 1980; LIND 1968; MÜNSTER-SWENDSEN 1968). *Colletes hederae* is much smaller than *C. cunicularius*, one of the largest bees in Germany with a mean heating rate of 7.35 °C per min (STONE & WILLMER 1989). Furthermore the activity is not only influenced by temperature but also by light intensity. KLOSTERMEYER (1969) and GERBER (1969) reported that the flight activity of bees stopped under a limit of 15000 lux. We did not measure light intensity but the activity of males and females was reduced when it was cloudy.

The first trip of the females was significantly longer than the other trips of the day. This can be interpreted as additional adult feeding on nectar after a night in the nest. Another reason may be a temperature threshold since the duration of the flights correlated negatively with temperature.

The results of the quantitative pollen analyses revealed on average five provisioning trips per cell. Thus *C. hederae* could provision one cell on an optimal day. A total of 18 bee days was estimated during which a female could provision by rule of thumb 18 cells. It has to be considered, though, that the summer and autumn were extraordinary warm and dry in 2003. Thus the females could not only use more days with optimal weather conditions for nest provisioning but also work faster because of high temperatures.

Summarising the results, the specialisation of *C. hederae* on a late blooming host plant seems to minimise the competition for pollen resources as well as for nest site resources. The risk of parasitism may also be reduced. These advantages may compensate the disadvantages of bad weather periods in autumn. It would be worthwhile to study also the diurnal foraging cycle and reproduction rate of the closely related species *C. halophilus* and *C. succinctus*, who may follow different strategies.

Acknowledgements. This work is dedicated to the late Prof. Dr. C. M. Naumann. We thank Prof. Dr. W. Böhme (ZFMK) for supporting this study and Priv. Doz. Dr. G. Welp and Evi Sillmann (Institute for Soil Science, University of Bonn) for the analysis of the soil samples. Further we wish to thank Axel Hirschfeld for help with statistical analyses. We are grateful to Dr. Rainer Hutterer and Dr. Bradley Sinclair who reviewed the manuscript. We are very much indebted to the following persons and institutions that provided us with distribution records: Felix Amiet, Solothurn, Yves Gonseth (Centre Suisse de Cartographie de la Faune, CSCF, Neuchatel), Willem Hogenes (Zoölogisch Museum Amsterdam), Stuart Roberts and Mike Edwards (Bees, Wasps and Ants Recording Society, BWARS) and Hans-Richard Schwenninger (Stuttgart).

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Bonner zoologische Beiträge | Band 53 (2004) | Heft 1/2 | Seiten 37–80 | Bonn, Juni 2005

The Phylogeny of Southeast Asian and Indo-Pacific Calicnemiinae (Odonata, Platycnemididae)[1]

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Abstract. Phylogenetic relationships of Southeast Asian and Indo-Pacific damselflies of the subfamily Calicnemiinae (Odonata: Platycnemididae) are examined by cladistic analyses using morphological characters. The strict consensus cladogram of the resulting equally most parsimonious trees supports the monophyly of the Papuan genus *Idiocnemis* Selys, the Philippine genus *Risiocnemis* Cowley and its subgenera, but leaves the basal relationships of the African genera and the Palawan genus *Asthenocnemis* Lieftinck partly unresolved. A preferred phylogenetic hypothesis is presented showing a well supported 'Indo-Pacific clade' consisting of Philippine, New Guinean and Solomon island taxa, and as sister group *Asthenocnemis*. *Risiocnemis* turns out to be a sister group of *Lieftinckia/Salomocnemis* (Solomon Islands), the sister taxon of those being the central New Guinean *Arrhenocnemis* Lieftinck. Together, these form a monophyletic group with the remaining Papuan taxa. *Idiocnemis leonorae* Lieftinck is transferred to *Rhyacocnemis* Lieftinck **comb. nov.** The possible effects of taxon sampling are discussed.

Key words. Taxonomy, biogeography, morphology, Southeast Asia, phylogeny, cladistic analysis, *Rhyacocnemis leonorae* **comb. nov**.

1. INTRODUCTION

The odonate subfamily Calicnemiinae Fraser, 1957 represents small to medium-sized damselflies (Zygoptera) inhabiting small running waters throughout the old world. The group is almost exclusively tropical. Due to the confinement to stable habitats and lacking dispersal capacities in the rainforest environment, the majority of species shows a high degree of endemism, both at species and genus level. Therefore, the group is well suited for historical biogeographical analyses (GASSMANN in prep.).

SELYS (1863) distinguished seven subgenera in his 'legion Platycnemis'. Together, those subgenera, which were later given generic rank by the same author (SELYS 1886) represented a large part of the Afrotropical, Southeast Asian and Indo-Pacific Calicnemiinae known today. TILLYARD (1917) raised SELYS' legions to subfamily level resulting among others in a subfamily Platycnemidinae (he used the incorrect name 'Platycneminae'). However, the family-group name had already been introduced earlier (YAKOBSON & BIANKI 1905). TILLYARD & FRASER (1938/40) finally erected the family Platycnemididae. In the most recent account on the group, MARTENS (1996) provided five diagnostic characters (at least with regard to Coenagrionidae) for the family: the comparatively long and obtuse discoidal cell (quadrilateral), the length of the pterostigma (matching no more than one wing cell), the variable position of arculus (at or distal to Ax2), the course of the longitudinal veins MA and IR3 (mainly straight, only apically zigzagged), and size (small to medium-sized). Another character of Platycnemididae, long ciliae on the legs, was already mentioned by Selys (1886) for his legion Platycnemis; however, this trait is shared by other zygopteran families (SCHMIDT 1951b).

The Platycnemididae now consist of two subfamilies, Platycnemidinae Yakobson & Bianki, 1905, and Calicnemiinae Fraser, 1957.

The subfamily Platycnemidinae

FRASER (1957) was the first to define the subfamily in its present form, containing the two genera *Platycnemis* Burmeister, 1839, and *Copera* Kirby, 1890. The dilation of the male tibiae, which is the most distinct feature Fraser used to characterize the subfamily, has turned out to be not diagnostic for the group. Several species currently assigned to Platycnemidinae, for example, some Madagascan ones (SCHMIDT 1951a) have undilated tibiae. Contrarily, one species of Calicnemiinae, *Risiocnemis atropurpurea* (Brauer), does have dilated tibiae.

Within the genus *Platycnemis*, 31 species are currently recognized (derived from MARTENS 1996 and HÄMÄLÄINEN 2003). The group exhibits a disjunct pattern of distribution, involving the western Palaearctic region, eastern Asia, northwestern/ western Africa as well as the Madagascan region (SCHMIDT 1951a; MARTENS 1996). No representatives were known from Southeast Asia until recently. However, the recent discovery of a new species from Laos (P. *phasmovolans* Hämäläinen) extends the distribution of the group far into the Indo-Chinese region (HÄMÄLÄINEN 2003).

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[1] In commemoration of Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004)

Within the genus *Copera* (*Copera* spec., Plate 1b) currently nine species are recognized (MARTENS 1996). The group is largely replacing *Platycnemis* in Southeast Asia, but there is an area of overlap in eastern Asia (MARTENS 1996). The generic borders between *Copera* and *Platycnemis* are weakly defined, and their identity recently has been put in question by HÄMÄLÄINEN (2003).

The subfamily Calicnemiinae

The damselfly subfamily Calicnemiinae was erected by FRASER (1957) to accomodate species of platycnemidid damselflies which did not fit into the subfamily Platycnemidinae. Fraser himself stated: "This subfamily is formed mainly for convenience to separate the true Platycnemiines, and one has only to compare the genera composing it, to note how artificial it appears to be...". Unfortunately, Fraser did not provide diagnostic characters for the subfamily, except for the absence of dilated tibiae, which on the other hand is a striking feature in the second subfamily Platycnemidinae. BECHLY (1996) found no autapomorphies for the group. Later authors (MARTENS 1996) have provided additional distinguishing characters for Calicnemiinae, i.e. the comparatively acute discoidal cell (quadrilateral) and the length of the anal vein.

The Calicnemiinae reach their highest diversity in Southeast Asia and the Indo-Pacific region. Remarkably, the group is absent from Wallacea (Sulawesi, Smaller Sunda Islands, Moluccas), which has been confirmed, at least for Sulawesi, by several odonatological surveys during the last decades (VAN TOL 2000).

The African genera of Calicnemiinae

The African genera of the subfamily are a rather heterogenous assemblage comprising only about a dozen species in total (SCHORR et al. 2004). The family status of some of them, in particular that of *Mesocnemis* Karsch, 1891 (Western Africa, 4 species) and *Metacnemis* Selys, 1863 (Southern Africa, Madagascar; 3 species), has been doubted (MARTENS 1996; WATERSTON 1984). Except for *Allocnemis* Selys, 1863 (Southern Africa, 2 species), all remaining African genera are monotypic: *Leptocnemis* Selys, 1886 and *Paracnemis* Martin, 1903 (Madagascar), *Oreocnemis* Pinhey, 1971 (eastern Africa) and *Arabicnemis* Waterston, 1984 (Arabian Peninsula). *Allocnemis* and *Arabicnemis* also extend into subtropical areas.

The Oriental genera of Calicnemiinae

From the Oriental region, four calicnemiine genera have been recognized. *Calicnemia* Strand, 1928 is a medium-sized genus with 17 described species (SCHORR et al. 2004) which reaches its highest diversity in the Himalayan region (LIEFTINCK 1984); however, its distributional range further extends southeast into the Indo-Chinese mainland as well as to Taiwan and Hainan. Interestingly, no representatives of *Calicnemia* are known from the Greater Sunda Islands. *Indocnemis* Laidlaw, 1917, is a monotypic genus; *I. orang* (Förster in Laidlaw, 1907) occurs in India and mainland Southeast Asia. *Coeliccia* Kirby, 1890 is by far the largest genus of Calicnemiinae, currently comprising 59 species according to SCHORR et al. (2004). Its distribution area ranges from the Himalayan region via the Southeast Asian mainland into the Greater Sunda Islands and even into the western and southwestern Philippines; south to the Philippines, along the Greater Sunda Islands, the eastern border of *Coeliccia* matches the Wallace line, except for the island of Bali from where no representative of the genus is known. A taxonomic and phylogenetic revision of a presumably monophyletic subgroup of the genus, consisting of Sundaland and Philippine taxa, is in work (DIJKSTRA & GASSMANN, in prep.). The fourth Oriental genus, *Sinocnemis*, comprises two species and was established quite recently (WILSON & WEN-BAO 2000); however, it could not be studied in detail for the present analysis.

The Indo-Pacific Calicnemiinae

Recently, a large part of the New Guinean and Philippine taxa have been revised taxonomically (GASSMANN 1999, 2000; GASSMANN & HÄMÄLÄINEN 2002; HÄMÄLÄINEN 1991a/b, 2000). Based on recently collected specimens from different sources, several new species were recognized. The New Guinean genus *Idiocnemis* Selys now amounts to 19 species and thus represents the largest genus in the Papuan region, followed by *Lieftinckia* Kimmins (Solomon Islands; 6 species), *Rhyacocnemis* Lieftinck (New Guinea; 3 species, see below), *Paramecocnemis* Lieftinck (New Guinea, 2 species). The remaining Papuan genera *Cyanocnemis* Lieftinck, *Lochmaeocnemis* Lieftinck, *Thaumatagrion* Lieftinck, *Torrenticnemis* Lieftinck (New Guinea) and *Salomocnemis* Lieftinck (Solomon Islands) are all monotypic (for *Arrhenocnemis* see below). The Philippine genus *Risiocnemis* Cowley now comprises 36 described species, with subgenus *Igneocnemis* Hämäläinen (20 species) being somewhat larger than the nominal subgenus *Risiocnemis* Cowley (GASSMANN & HÄMÄLÄINEN 2002). Within the Philippine Calicnemiinae, the Palawan genus *Asthenocnemis* Lieftinck is an outstanding representative. Originally, Lieftinck thought that the peculiar female specimen from the Martin collection of which he based the description of the new species, *A. stephanodera*, would originate from New Guinea (LIEFTINCK 1949). Later, with the arrival of additional (male) specimens from Palawan Island, he stated his error (LIEFTINCK 1971, 1974).

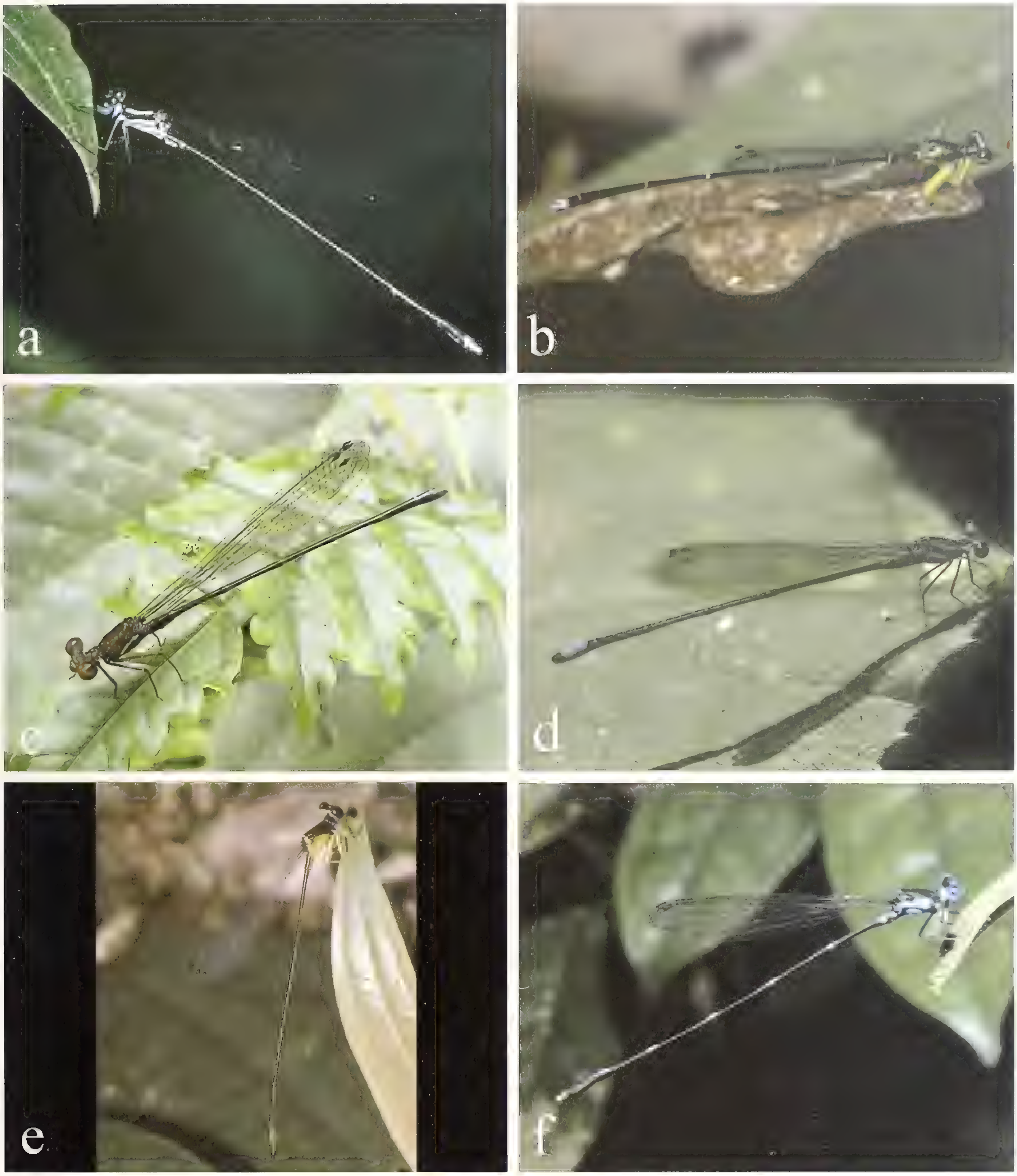


Plate 1: a) *Coeliccia membranipes*, ♂, Java; Photo: J. van Tol. b) *Copera* spec., ♂, Sarawak, Borneo; Photo: D. Paulson. c) *Idiocnemis australis*, ♂, Lake Kutubu, Papua New Guinea; Photo: J. Michalski. d) *Idiocnemis inaequidens*, ♂, Morobe Province, Papua New Guinea; Photo: D. Gassmann. e) *Risiocnemis kaiseri*, ♂, Samar, Philippines; Photo: R. A. Müller. f) *Risiocnemis serrata*, ♂, Luzon, Philippines; Photo: D. Paulson.

Preexisting hypotheses on phylogenetic relationships within Calicnemiinae

Several authors have occasionally discussed the presumed relationships between different genera of Calicnemiinae (FRASER 1932; LIEFTINCK 1958, 1963). Since these considerations were not yet influenced by the methodological tools provided by W. HENNIG'S phylogenetic systematics (1950, 1966), they were determined to remain rather vague assumptions which were not necessarily founded on synapomorphic traits (see discussion). Also FRASER's 'reclassification of Odonata' (1957) is not based on cladistic concepts, and up to now no phylogenetic study on platycnemidid damselflies has been available. However, BECHLY (1996) and recently REHN (2003) performed morphological-phylogenetic higher-level analyses of Odonata, including some selected representatives of the superfamily Coenagrionoidea, respectively.

2. MATERIALS AND METHODS

2.1. Specimens examined

The present study is based on preceding revisional work on the taxonomy of Papuan and Philippine Calicnemiinae by GASSMANN (1999, 2000) and GASSMANN & HÄMÄLÄINEN (2002). The reader is referred to those references for detailed material lists. However, in the meantime, many additional taxa, among them the entire subgenus *Risiocnemis*, have been studied for a more inclusive analysis of phylogenetic relationships between the Indo-Pacific representatives of the subfamily; those specimens are listed in Appendix 4. Despite the fact that they are not yet formally described, the male of *Risiocnemis moroensis* as well as the females of *R. gracilis* and *Idiocnemis leonorae* have been included in the analysis.

2.2. Taxon sampling

Relationships between the Indo-Pacific taxa were examined down to species level; all the known species were included (Appendix 1). However, for the Oriental genera, in particular the huge genus *Coeliccia* Kirby, 1890, this was not possible due to practical constraints. Thus, for both the Oriental and the African genera, only single representatives were included in the analysis. *Thaumatagrion funereum* from New Guinea was examined, but finally not included in the analysis, because its current status within Platycnemididae should be seriously doubted (see results and discussion). On the other hand, the author did not see any reason not to include the two known *Arrhenocnemis* species; their habitus and wing venational characters - especially the distinctly crenulate wing margin - strongly resembles the Calicnemiinae (although Lieftinck considered them to belong to the Megapodagrionidae (LIEFTINCK 1965, 1971; see discussion)). Due to the lack (or limited availability) of material, the African genera *Metacnemis* Selys, 1863 and *Oreocnemis* Pinhey, 1971 as well as the comparatively recently described Oriental genus *Sinocnemis* Wilson and Wen-bao, 2000 had to be excluded from the analysis. It should be noted that currently also phylogenetic revisions of *Calicnemia* Strand, 1928 (GASSMANN, in prep.) and the Philippine and Bornean representatives of *Asthenocnemis* and *Coeliccia* (DIJKSTRA & GASSMANN, in prep.) are in work, eventually providing a better understanding of the West Malesian calicnemiine fauna.

2.3. Outgroup choice

The second subfamily of Platycnemididae and presumed sister group of Calicnemiinae, the Platycnemidinae, were chosen as outgroup for the analysis. Unfortunately, it was not possible to include more taxa than one representative for each of the two genera *Platycnemis* and *Copera*; however, a literature survey revealed that the majority of species within Platycnemidinae are at least structurally very similar (e.g. SCHMIDT 1951a).

2.4. Scanning electron microscopy (SEM)

The male ligulae of almost all species and the male appendages and female prothoracices of selected species were examined by scanning electron microscopy (SEM). The scanning electron micrographs were taken by the author, mainly using a JEOL SEM 6400 microscope. The objects were cleaned in 70% ethanol, air-dried and subsequently sputtered with gold for 1.5 - 2.0 min at 20 mA before examination. Figures 5-6, 9-10, 17-18, 19-20, 23-24 and 35-36 were made using a JEOL SEM 840A microscope.

2.5. Terminology

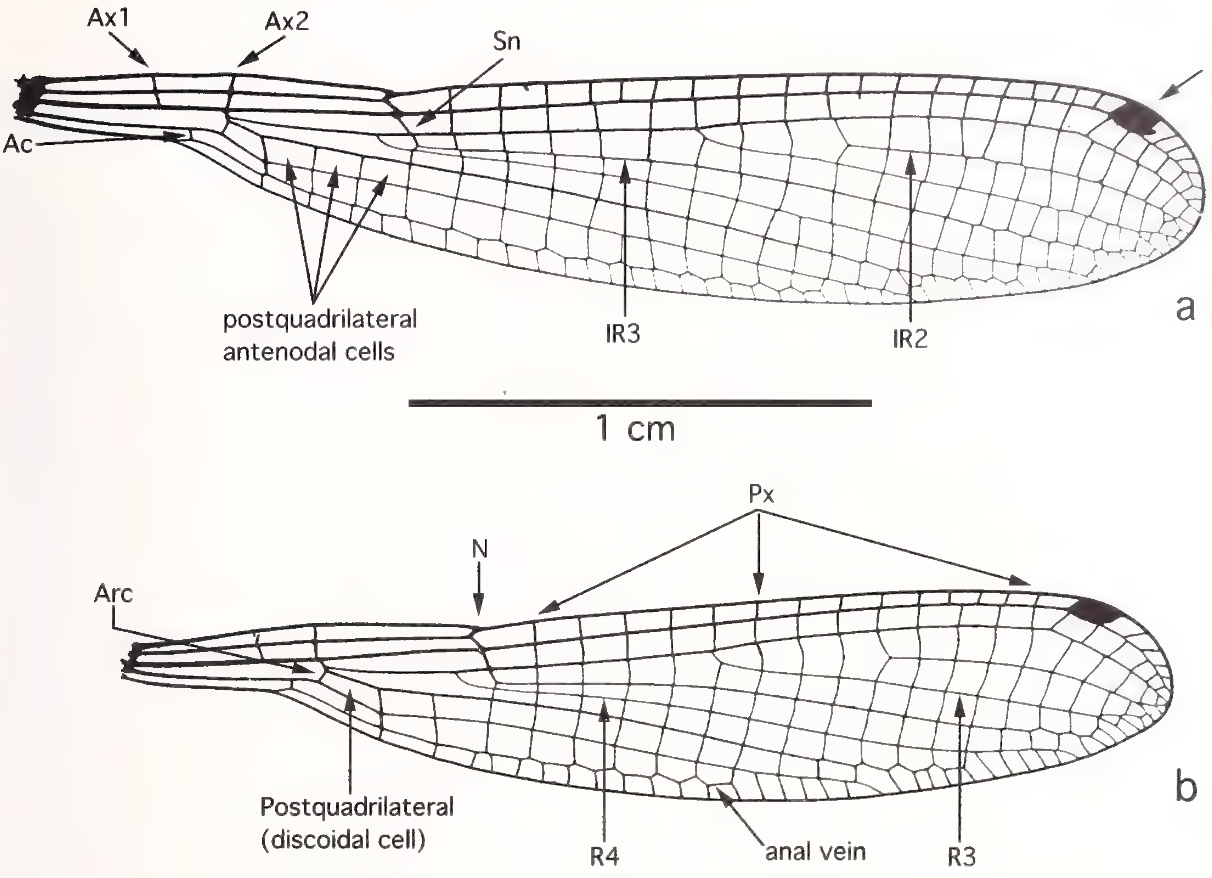
Although the modified Tillyard-Fraser system of odonate wing venation (cf. WATSON & O'FARRELL 1991) is controversial (loc. cit.), it is further applied here, because it has already been used in preceding revisional work on Calicnemiinae (GASSMANN 1999, 2000; GASSMANN & HÄMÄLÄINEN 2002).

2.6. Measurements

The measurements of wings and abdomens were taken within a precision of 0.5 mm. Measurements of the additional specimens examined for the present paper are not given here but can be obtained from the author. In a few cases, measurements had to be taken from the literature.

2.7. Character coding

In several cases, coding of character states for the cladistic analysis was problematic, because an unambigious (i.e. objective) delimitation of discrete states was not possible. However, the attempt was made to divide, for instance, a gradually changing character into a


Ax1
Ax2
Sn
Pt
Ac
postquadrilateral antenodal cells
IR3
IR2
a
1 cm
Px
N
Arc
Postquadrilateral (discoidal cell)
R4
anal vein
R3
b

1

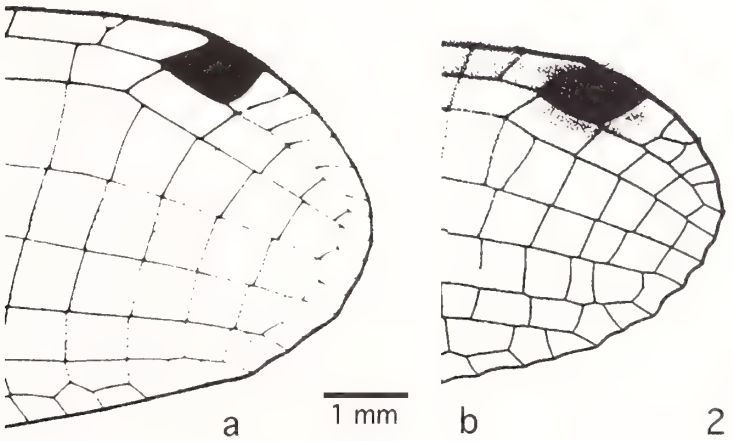


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Fig. 1: Left forewing of *Calicnemia eximia*, ♂ (a) and *Platycnemis pennipes*, ♂ (b). Abbreviations: Ac = antenodal crossvein; Arc = arculus; Ax = antenodal vein; N = nodus; Px = postnodal vein; Pt = pterostigma; (I)R = (intercalary) radius; Sn = subnodal vein.

Fig. 2: Wing apex of *Risiocnemis (Igneocnemis) tendipes*, ♂, (a), *Risiocnemis (Risiocnemis) laguna*, ♂, (b).

series of discrete intervals which were chosen as small and precise as possible (cf. character 56). For the treatment of continuous morphometrical traits: cf. characters 17 and 55.

Polymorphisms were entered as separate character states (scaled coding; different methods reviewed in WIENS 1999 and KORNET & TURNER 1999), but left unordered. However, in a few cases in which character states were not unambigiously codable (e.g. colour traits of deteriorated specimens), the states concerned were entered as polymorphies while applying the 'uncertainty' option in PAUP (SWOFFORD & BEGLE 1993) to minimize the potential effect of erroneously delimitated character states on the analysis.

2.8. Cladistic analysis

Morphological characters of imagines were compiled in a data matrix which consisted of 88 binary and multistate characters (listed below); due to our scarce knowledge of larval forms and the probably doubtful assignment of larval to adult specimens in the literature, larval characters were not considered for the present analysis. Since the female sex is unknown in several species, only three female characters were used to keep the amount of missing values in the data matrix low. In cases of characters exhibiting more than nine states, the consecutive states were labelled with Roman capital letters in the data matrix (Appendix 2); however, in the character list below, all states are numbered numerically for better readability. Four uninformative characters were excluded from the analysis. A parsimony analysis using PAUP* 4.0b4a (SWOFFORD 2002) was applied to examine relationships of 84 taxa in total. The resulting topology was rooted a posteriori by designating 2 taxa (see above) as outgroup. The heuristic search settings were chosen as follows: all characters unordered and equally weighted, starting tree(s) obtained via stepwise addition, random addition sequence with 100 replicates; branch-swapping algorithm: tree-bisection-reconnection (TBR). Character optimization was performed by accelerated transformation (ACCTRAN); character evolution was traced and examined by applying MacClade 3.04 (MADDISON & MADDISON, 1993): see Appendix 3. Analyses testing clade stability were performed using Autodecay 4.0 (ERIKSSON 1998) and PAUP* 4.0b4a (SWOFFORD 2002), the latter run under the same settings as above, but with only 10 replicates.The trees were rooted by applying the paraphyletic rooting option to avoid assignment of many ambiguous character states to the ingroup node while using only two outgroup taxa.

2.9. List of characters

Male characters:

Wings

1. Apical wing margin: shape.

(0) not crenulate (Fig. 1a/b); (1) smoothly sinuous (Fig. 2a); (2) distinctly crenulate (Fig. 2b).

All Papuan representatives of Calicnemiinae (but see below for *Thaumatagrion funereum*) as well as the species of subgenus *Risiocnemis* have a distinctly crenulate apical wing margin: from the level of the pterostigma up to about the distal third of posterior margin. The wing apex is furnished with concave inlets between the vein endings (Fig. 2b). Contrarily, the wing apex of *Igneocnemis* species is smoothly sinuous ('smoothly crenulate' in GASSMANN 1999, 2000 and GASSMANN & HÄMÄLÄINEN 2002): the posterior half of the apical wing margin is divided into shallowly deepened or, occasionally, straight areas, divided by more or less distinct emarginations at the levels of veins R_2, R_3, R_4 and - more proximal and less distinct - at CuP (Fig. 2a). This feature is largely shared by *Leptocnemis cyanops* from the Seychelles; however, it is slightly less distinct in that species and lacking the emargination at R_2.

2. Wing petiolation.

(0) between Ax1 and Ax2 (Fig. 1a/b); (1) proximal to Ax1.

In most species examined, the basal petiolation of the wings reaches up to a level just distal to the first antenodal crossvein (Ax1). Only in *Arabicnemis caerulea* and *Mesocnemis singularis*, the level of petiolation ends proximally to the level of Ax1.

3. Position of anal crossvein (Ac).

(0) distinctly distal to Ab (Fig. 1a/b); (1) at or slightly distal/proximal to Ab (about halfway between Ax1 and Ax2); (2) somewhat proximal to Ab (closer to Ax1 than to Ax2); (3) far proximal to Ab.

The position of the anal crossvein (Ac) relative to the insertion of the anal bridge (Ab) can be readily classified in distinct character states; however, there is some variation in those taxa showing condition (0): in *Mesocnemis singularis* and *Paracnemis alluaudi*, Ac is situated about 2.5 to 3.5 times its own length distal to Ab, whilst in other taxa as in *Cyanocnemis aureofrons*, the distance amounts to just about the length of Ac. *Lieftinckia* species have Ac situated far proximal to Ab, i. e. about halfway between wing base and Ax2.

4. Anal vein: length.

(0) short, reaching no further than up to about the level of Px6 (Fig. 1b); (1) long, reaching further than the level of Px6 (Fig. 1a).

The condition (0) usually means that R3 inserts at the level where the anal vein ends: a character originally used to dicriminate between the two subfamilies of Platycnemididae (MARTENS 1996; see also Fig. 1). However, the relation between these two veins cannot be applied to taxa where R3 and IR2 appear to be moved much more distally, as in *Risiocnemis* and some species of *Lieftinckia*. Therefore, in the present study the length of the anal vein is put in relation to the corresponding number of Px.

5. Arculus: position.

(0) proximal to Ax2; (1) at or slightly proximal to Ax2; (2) at Ax2 (Fig.1a); (3) at or distal to Ax2; (4) distal to Ax2.

The position of the arculus relative to the second antenodal vein (Ax2) has often been used as a taxonomic character in platycnemidid classification; however, the degree of variation differs between different genera.

6. Medio-anal link.

(0) straight or nearly straight (Fig.1b); (1) straight or slightly hooked; (2) slightly hooked (Fig. 1a); (3) distinctly hooked.

The shape of the medio-anal link corresponds with the shape of the quadrilateral: the posterior distal angle of the latter can be either nearly right, or very acute; consequently, the medio-anal link appears either straight or broken.

7. Third postquadrangular cell (forewing).

(0) absent (Fig. 1b); (1) absent or present; (2) present (Fig. 1a).

Both in forewing and hindwing, the majority of the examined species has two cells between quadrilateral and the vein descending from the subnodal vein. However, in some taxa the number of postquadrilateral cells can amount to three or four cells.

8. Fourth postquadrangular cell (forewing).

(0) absent; (1) absent or present; (2) present.

9. Third postquadrangular cell (hindwing).

(0) absent; (1) absent or present; (2) present.

10. Fourth postquadrangular cell (hindwing).

(0) absent; (1) present.

11. Position of R4 (forewing).

(0) distinctly proximal to Sn (Fig. 1a/b); (1) slightly proximal to Sn; (2) at Sn; (3) at or distal to Sn; (4) distal to Sn.

12. Position of IR3 (forewing).

(0) at Sn (Fig. 1a/b); (1) slightly distal to Sn; (2) between Px1 and Px2; (3) at about the level of Px2; (4) between Px3 and Px7.

13. R4 and IR3: fused/separate.

(0) separate; (1) fused at base.

In *Paramecocnemis*, the R4 and IR3 veins are fused from shortly distal to wing base up to about the level of Px1 to Px2. In all remaining taxa, the two veins are distinctly separate.

14. Pterostigma (forewing): length.

(0) matching one cell or less (Fig. 1b); (1) reaching well beyond one cell (Fig. 1a).

The length of the pterostigma was examined in relation to the posteriorly neighbouring cell.

15. Pterostigma (forewing): colour.

(0) brown; (1) white.

16. Wing colour.

(0) entirely clear; (1) with a slight brownish breath; (2) brownish at base; (3) entirely brownish.

17. Hind wing length.

(0) short (mean value = 17.0); (1) medium-sized (mean values = 19.6-29.4); (2) long (mean value = 30.7); (3) very long (mean value = 32.2).

To transform the measurement values into discrete states, gap-coding as described by ARCHIE (1985) was applied. The pooled within-group standard deviation (s_p) was calculated, and the group means (of species) were arranged by size; subsequently, every sub-row of means which leaves a gap greater than s_p (= 1.0) to neigbouring mean values, is assigned an integer score, respectively. *Arrhenocnemis sinuatipennis* was not considered, because only one measurement value (from the literature) was available.

Head

18. Labrum: ground colour.

(0) black; (1) dark brown; (2) reddish-brown; (3) yellow-orange; (4) yellow or yellowish-white; (5) bright red; (6) blue; (7) bluish-grey; (8) greenish-blue.

19. Anteclypeus: ground colour.

(0) black; (1) dark brown to black; (2) dark brown; (3) medium to dark brown; (4) medium brown; (5) light to medium brown; (6) light brown; (7) reddish-brown; (8) reddish-brown to black; (9) orange-brown; (10) yellow-orange; (11) yellowish or yellowish-white; (12) blue; (13) bluish-grey; (14) green.

20. Postclypeus: ground colour.

(0) black; (1) black, basal area orange; (2) dark brown to black; (3) dark brown.

(4) medium to dark brown; (5) medium brown; (6) reddish-brown; (7) orange-brown; (8) orange; (9) blue; (10) bluish-grey; (11) green.

21. Genae: colour.

(0) black; (1) dark brown; (2) reddish-brown; (3) light to medium brown; (4) yellow-orange; (5) greenish-yellow; (6) greenish-blue; (7) bluish-grey; (8) blue.

22. Postclypeus: shape (in lateral view).

(0) bulgy, edge rounded; (1) slightly curved, edge bulgy; (2) slightly curved, edge semi-sharp; (3) angulate, edge sharp.

23. Frontal stripe.

(0) present; (1) absent.

The anterior part of the head may show several kinds of distinct or diffuse markings. A comparatively distinct feature is the frontal stripe which, if present, runs from eye to eye (for an exception see below), covering the frons and the parts lateral to it.

24. Frontal stripe: extension.

(0) reaching to a level just anterior to antennae, not including antennal sockets; (1) up to and including antennal sockets; (2) up to and including antennal scapus.

In *Asthenocnemis stephanodera*, as an exception, the frontal stripe is not reaching the eye margin, respectively, but instead is only slightly exceeding the width of postclypeus.

25. Frontal stripe: shape.

(0) more or less complete, not interrupted; (1) interrupted in the center of frons.

26. Frontal stripe: colour.

(0) reddish-brown; (1) blue; (2) greenish-blue; (3) greenish-yellow; (4) bluish-grey to violet; (5) orange; (6) pale orange; (7) chrome.

27. Brown stripes lateral to postclypeus.

(0) present, reaching from postclypeus to eye margin; (1) short, rudimentary, reaching only halfway the distance from postclypeus to eye margin; (2) absent.

The character state is coded as unknown for those taxa in which the lower anterior part of the head is black throughout, so that no discrete stripes are recognizable.

28. Vertical stripe at the level of ocellar area.

(0) present; (1) reduced to a pair of transverse elongate spots; (2) reduced to a pair of longitudinal elongate spots; (3) reduced to diffuse stripe; (4) absent.

29. Vertex: ground colour.

(0) black; (1) black to reddish-brown; (2) reddish-brown to bright red; (3) bluish-grey.

30. Antennal scapus: ground colour.

(0) black; (1) dark brown; (2) reddish-brown; (3) light brown; (4) orange; (5) bright red; (6) yellow-white; (7) bluish-grey; (8) blue.

31. Antennal pedicellus: ground colour.

(0) black; (1) dark brown; (2) reddish-brown; (3) light brown; (4) orange; (5) bright red; (6) yellow-white; (7) bluish-grey; (8) blue.

32. Length ratio antennal pedicellus/scapus.

(0) subequal in length; (1) about 1.25 times the length; (2) about 1.5 times the length; (3) about twice the length; (4) about 2.5 times the length; (5) about 3 times the length.

33. Subquadrangular marking around ocelli.

(0) absent; (1) present.

Except for *I. nigriventris*, the vertex of species of the *Idiocnemis bidentata* species-group is marked by a subquadrangular black marking (cf. GASSMANN 2000, fig. 31).

34. Postocellar spots on vertex.

(0) absent; (1) small, circular, framed; (2) large, subtriangular; (3) very large, subtriangular.

35. Distinct elongate spots on occiput.

(0) present; (1) absent.

36. Brown spots lateral to ocelli.

(0) absent; (1) present.

Thorax

37. (Male) pronotal tubercles: size.

(0) flat or only slightly raised; (1) distinct; (2) very distinct.

Males of most taxa studied have the right and left half of the median lobe either not raised or only slightly rounded in lateral view. However, they can be raised to distinct protrusions, reaching their extreme in *Asthenocnemis stephanodera.*

38. Prothorax: ground colour.

(0) black or brown-black; (1) brown-black; (2) light, reddish- or medium brown.

39. Legs: coloration.

(0) Black throughout or mainly black; (1) mainly black or dark brown; (2) light to medium brown, darkened to a varying extent; (3) yellow-light brown with black markings; (4) yellow-brown or -black; (5) red-black; (6) bright orange; (7) orange-red; (8) black-bluish(-white).

40. Legs: shape of tibiae.

(0) distinctly dilated; (1) not distinctly dilated.

41. Synthorax: robust mesonotal processes.

(0) absent; (1) present.

Arrhenocnemis amphidactylis shows a conspicuous, finger-like outgrowth at either side of dorsal carina of anterior part of synthorax.

42. Synthorax: black line/marking on dorsal carina.

(0) narrow; (1) broad; (2) dorsal surface of synthorax black or brown-black throughout (except for antehumeral stripes, if present).

The extension of black coloration on synthorax is either restricted to the dorsal carina, or it fills the entire upper surface of synthorax (occasionally reaching beyond the humeral suture). In *Idiocnemis dagnyae*, as an exception, the black carinal stripe varies in width from exactly matching the median carina up to reaching the width of the carinal forks.

43. Antehumeral stripe.

(0) complete stripe; (1) distinct, interrupted; (2) half stripe; (3) short anterior stripe, joining humeral suture (4) distinct, reduced to anterior spot, joining carinal fork; (5) rudimentary, interrupted; (6) diffuse stripe; (7) absent.

44. Metepisternal stripe.

(0) absent; (1) rudimentary; (2) present.

45. Metepisternal stripe: colour.

(0) blue; (1) turquoise; (2) diffuse light brown; (3) greyish-purple; (4) orange; (5) bluish-grey; (6) green, intermingled with orange; (7) yellowish.

46. Distinct metepimeral marking.

(0) not clearly defined; (1) short, subquadrangular.

This feature is included here to characterize some species of subgenus *Risiocnemis* of which the metepimera are furnished with distinct subquadrangular colour markings (see HÄMÄLÄINEN 1991a). In the remaining taxa, the metepimeron is either entirely or largely uniform in coloration.

47. Meso- and metathoracic markings.

(0) absent; (1) present.

In some species of the *inornata* species-group of *Idiocnemis*, the mes- and metepisternal fossae at posterior ends of first and second lateral sutures are covered by an elongate black spot, respectively. This character was examined and scored only for *Idiocnemis* species.

48. Pruinescence

(0) absent; (1) parts of head, pro- and synthorax and legs pruinescent; (2) pruinescent throughout.

49. Underside of synthorax: bristles.

(0) absent or only minute; (1) a well-delimited patch of robust spines present.

Abdomen

50. Abdomen: basic colour pattern.

(0) rather uniform (often with more or less distinct annules), but lacking a clear separation in two different colours; (1) abdomen distinctly separated in anterior (brown-)black and posterior reddish part.

51. Posterior dorsal abdominal marking: colour.

(0) blue to violet/purple; (1) yellow-orange or yellow-white; (2) blue-whitish-pruinescent.

A variably shaped, mostly subquadrangular colour marking covers the dorsal surface of last abdominal segments in several taxa studied.

52. Dorsal marking on segment 9.

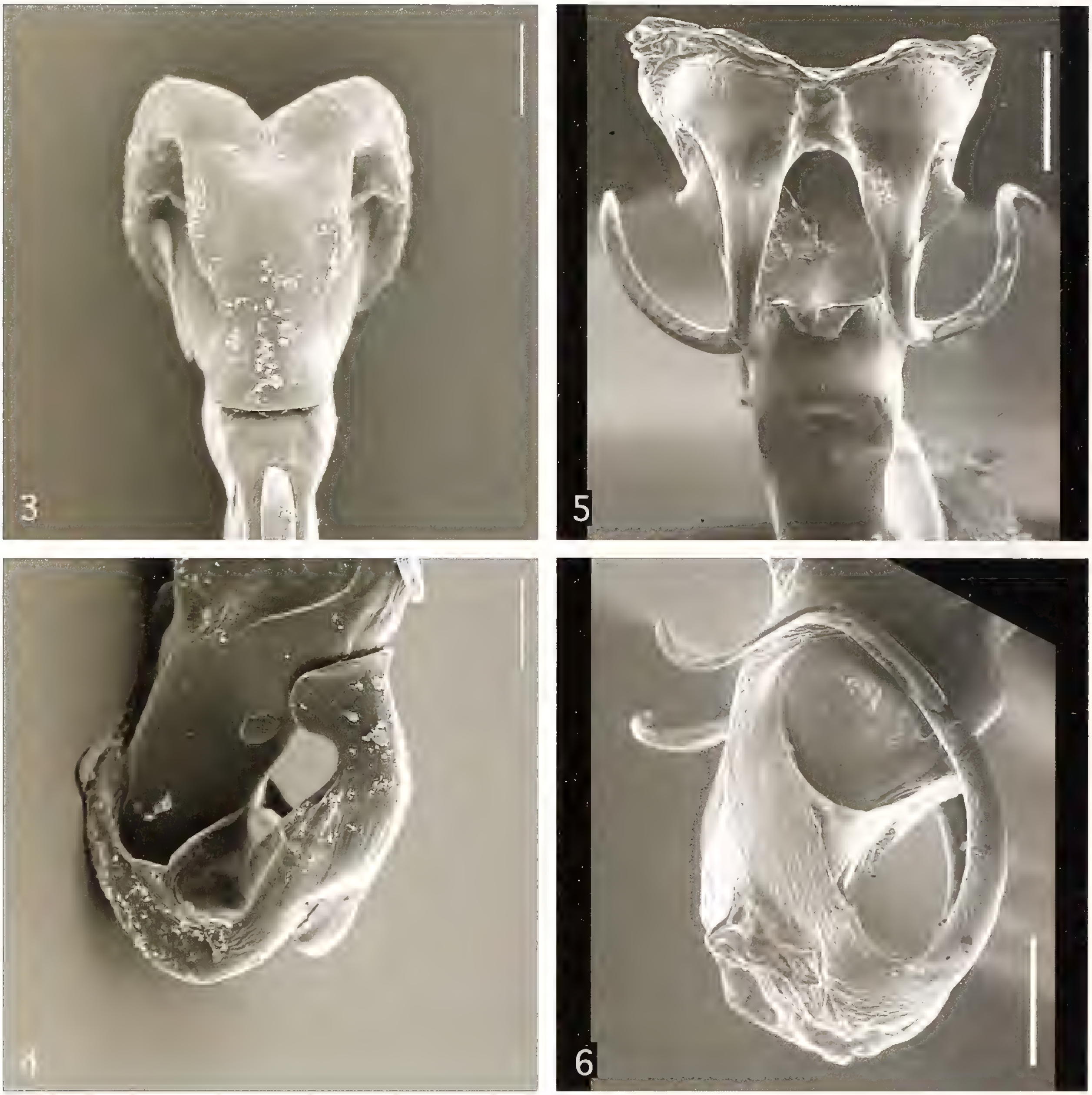
(0) absent; (1) present.

53. Dorsal marking on segment 10.

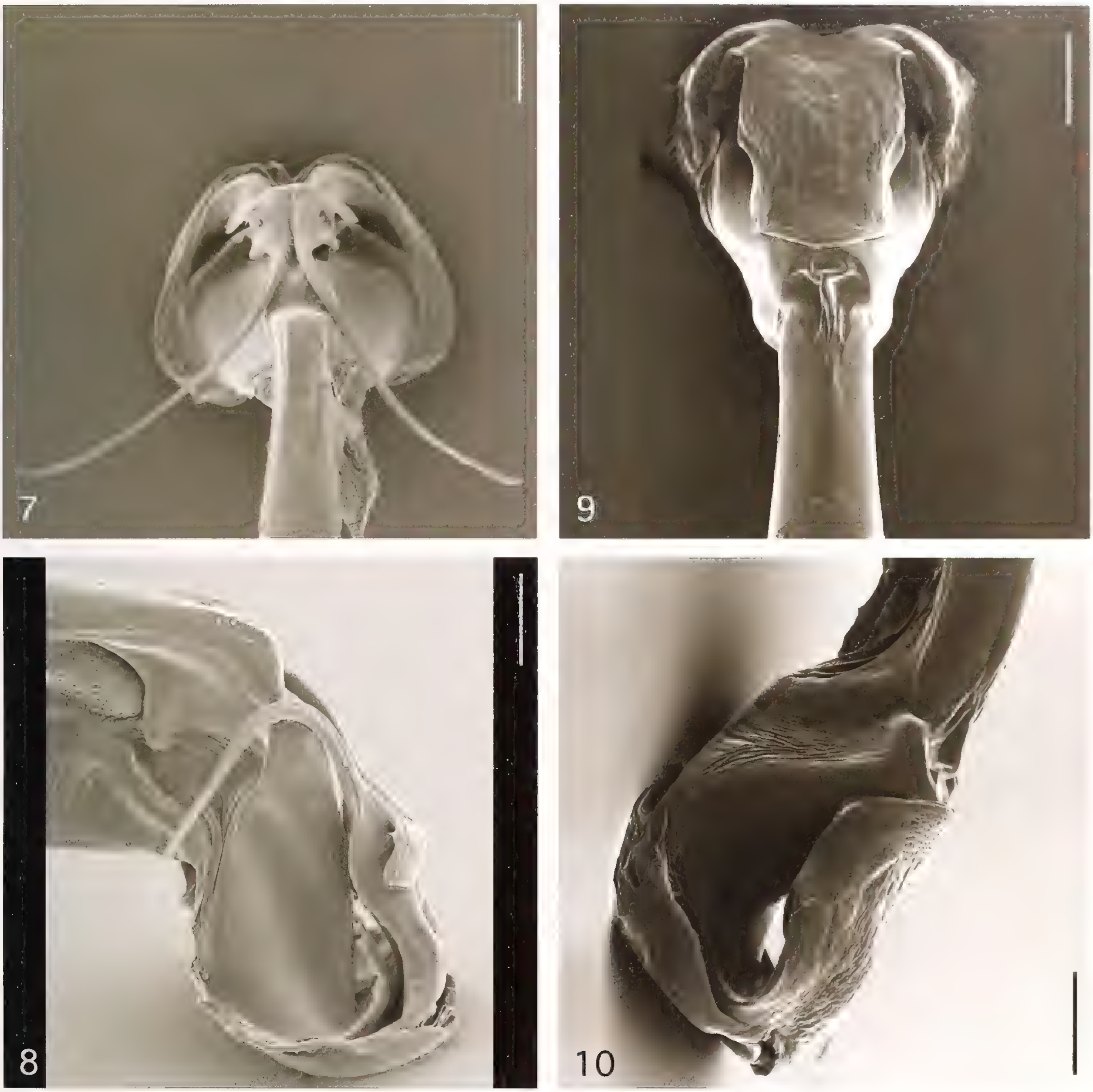
(0) absent; (1) present.

54. Terminal abdominal segments: shape.

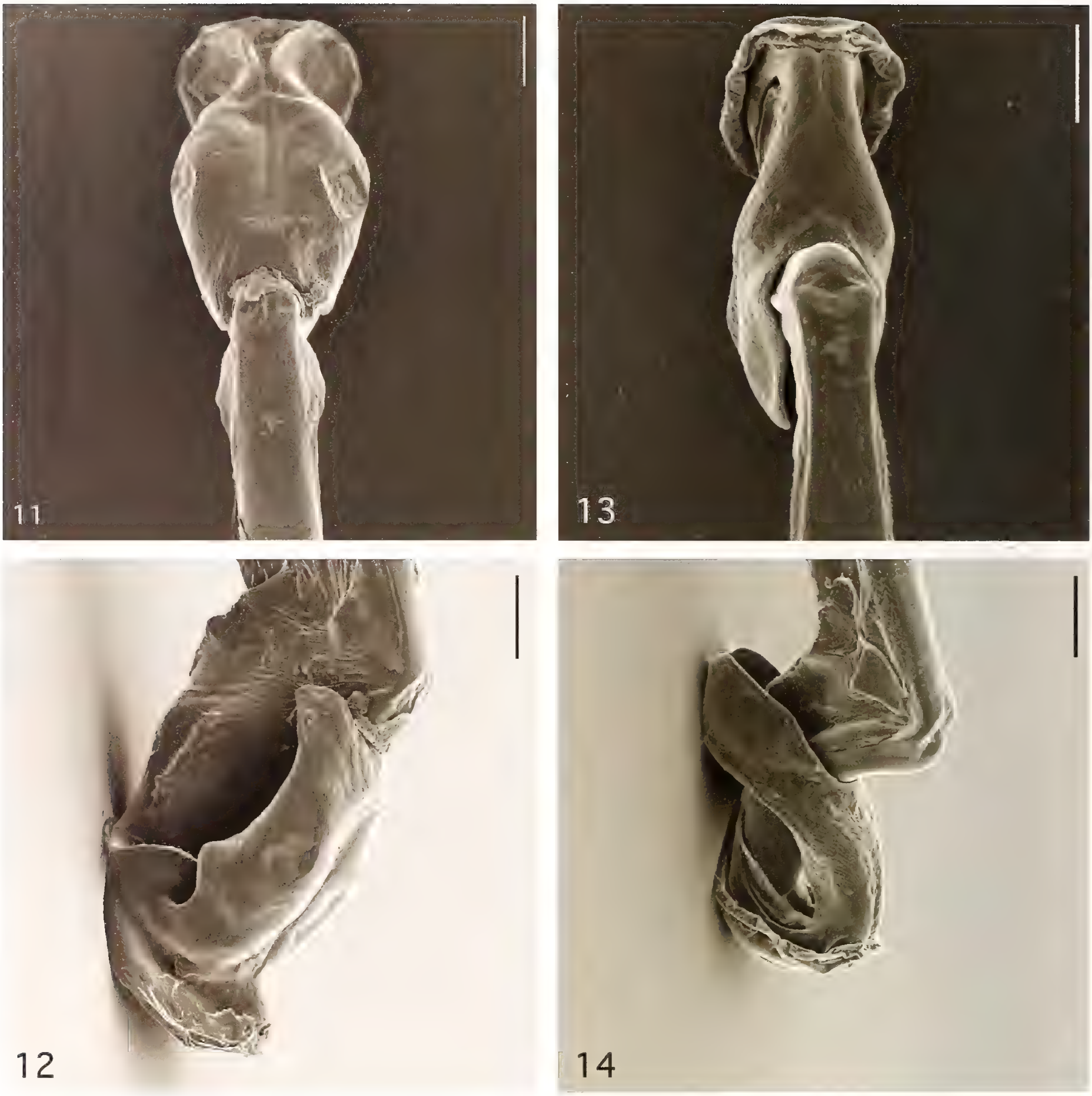
(0) not or only slightly inflated; (1) distinctly inflated.



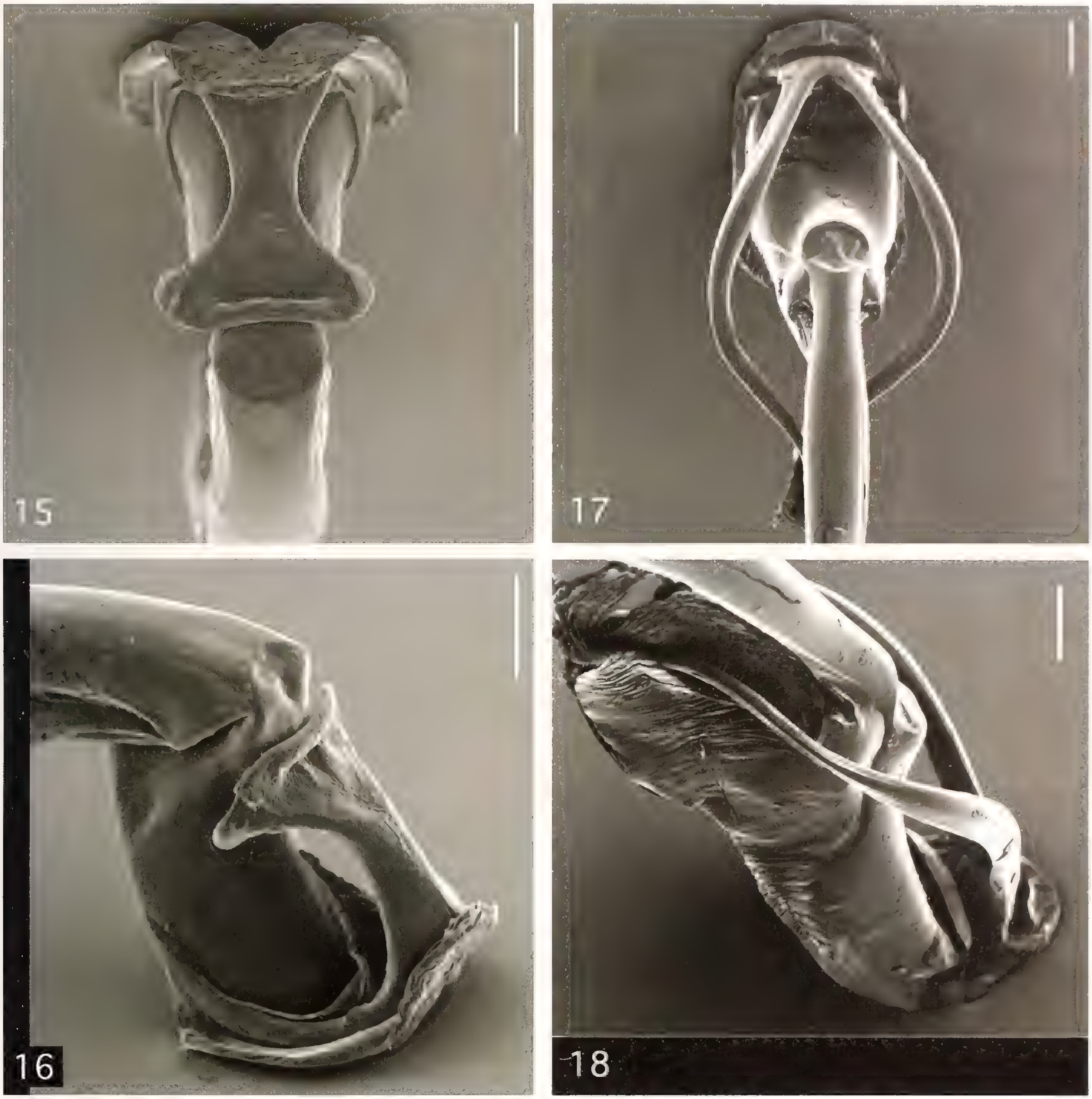
Figs. 3-6: Ligulae of ♂♂ in ventral (3, 5) and lateral view (4, 6): 3-4, *Asthenocnemis stephanodera*; 5-6, *Calicnemia eximia*. Scale bars 100 µm



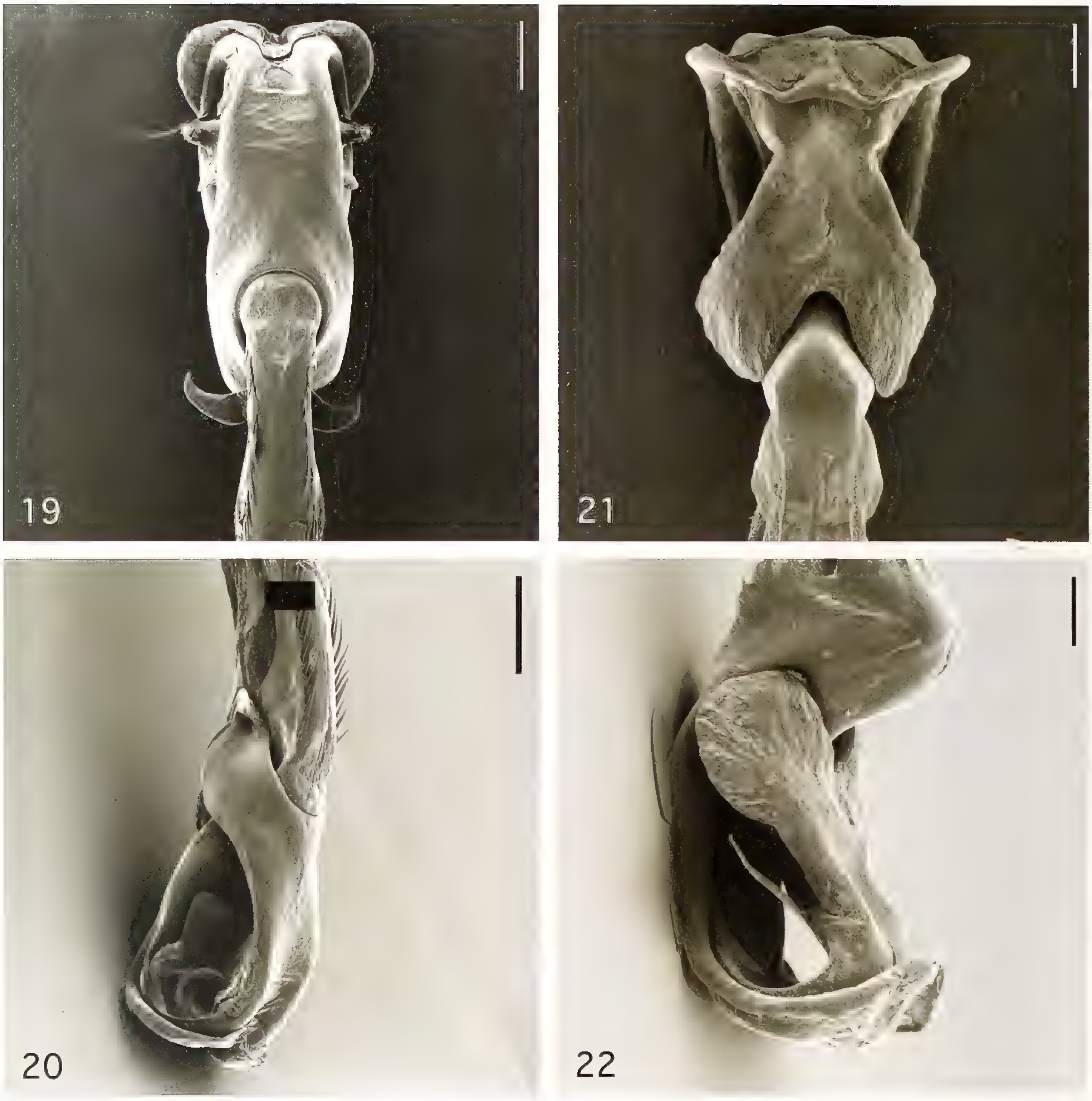
Figs. 7-10: Ligulae of ♂♂ in ventral (7, 9) and lateral view (8, 10): 7-8, *Coeliccia membranipes*; 9-10, *Copera marginipes*. Scale bars 100 µm.



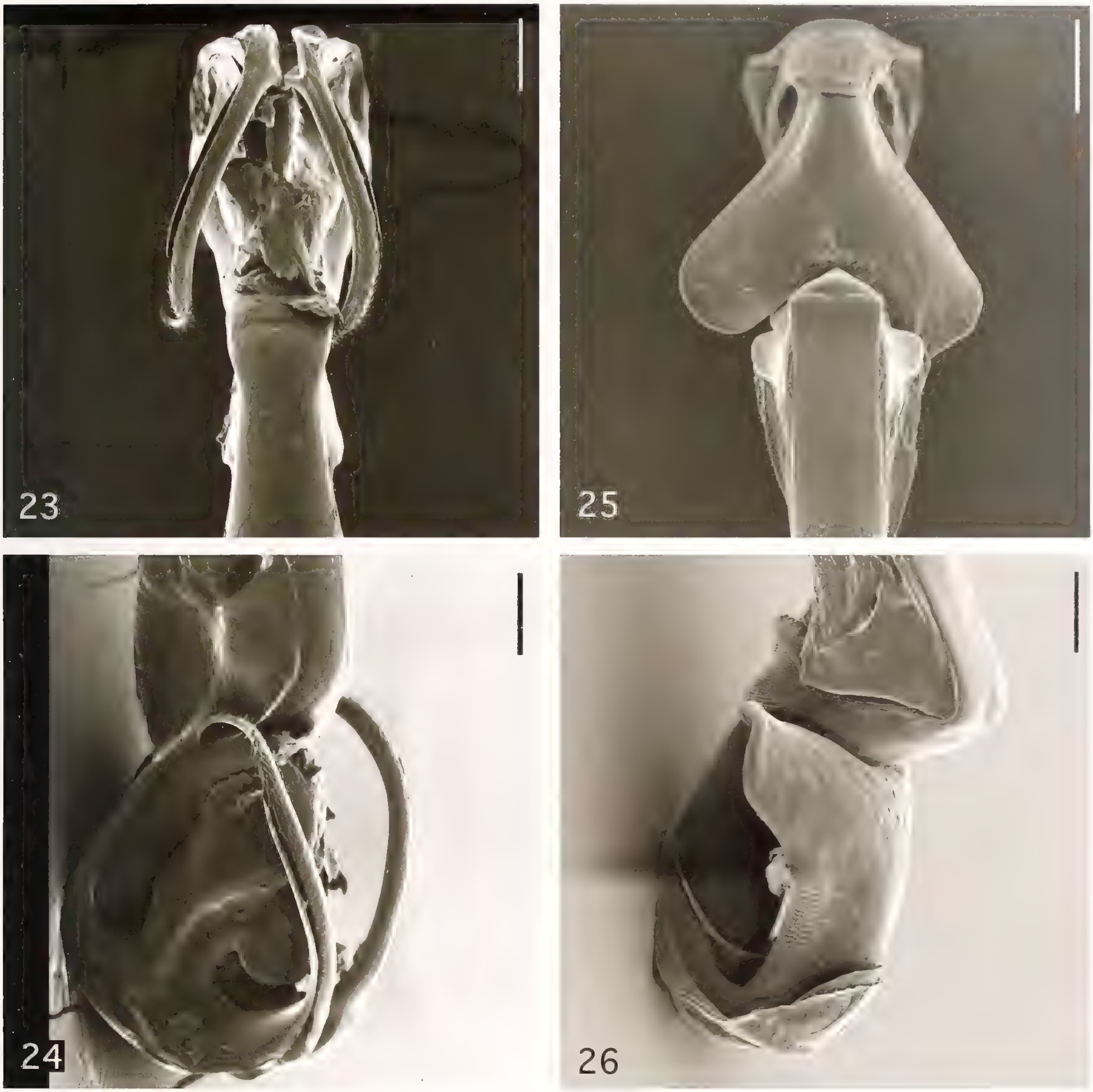
Figs. 11-14: Ligulae of ♂♂ in ventral (11, 13) and lateral view (12, 14): 11-12, *Cyanocnemis aureofrons*; 13-14, *Idiocnemis polhemi* (from alt. 700 m). Scale bars 100 µm.



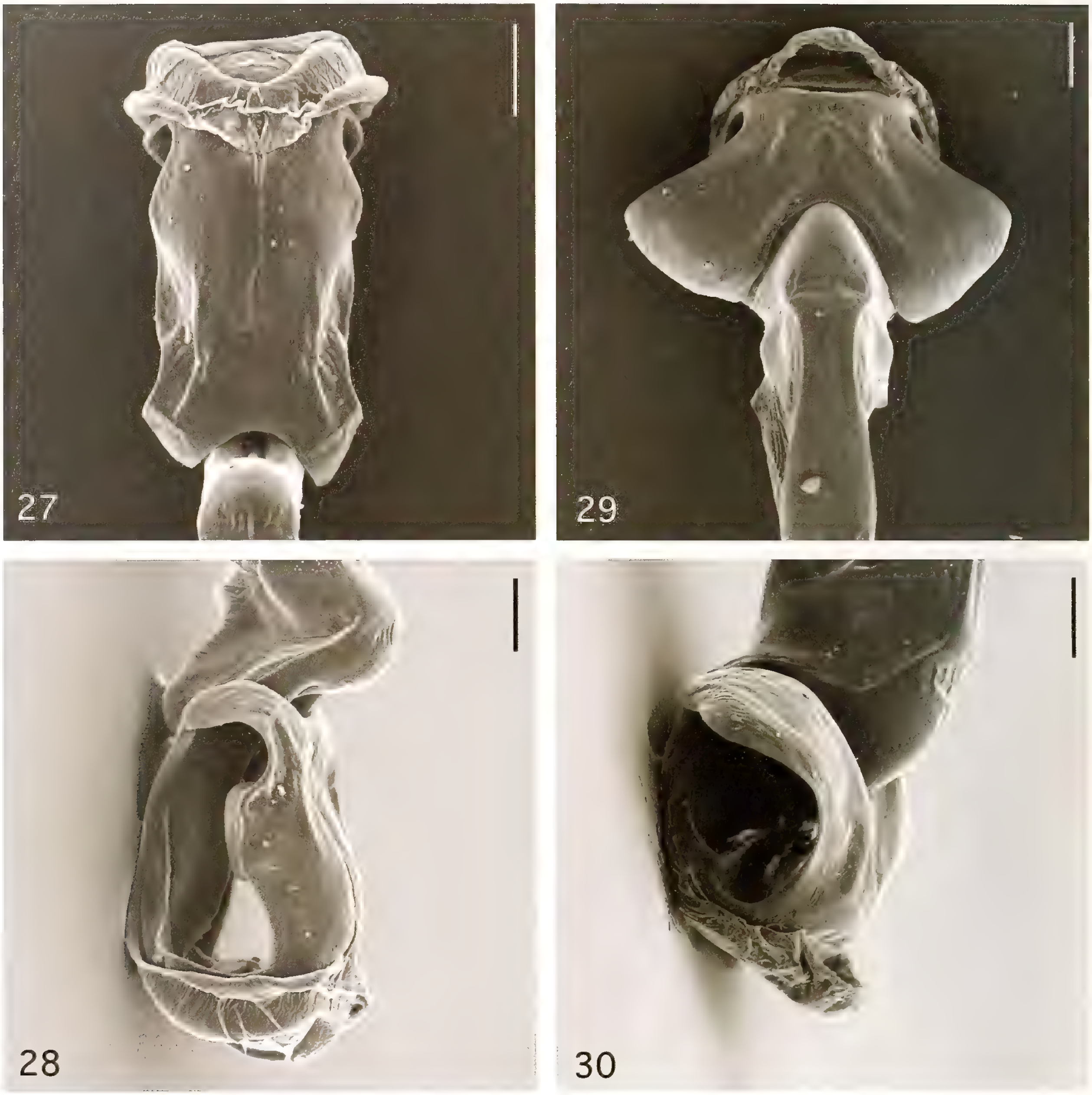
Figs. 15-18: Ligulae of ♂♂ in ventral (15, 17) and lateral view (16, 18): 15-16, *Idiocnemis zebrina sufficiens*; 17-18, *Indocnemis orang*. Scale bars 100 µm.



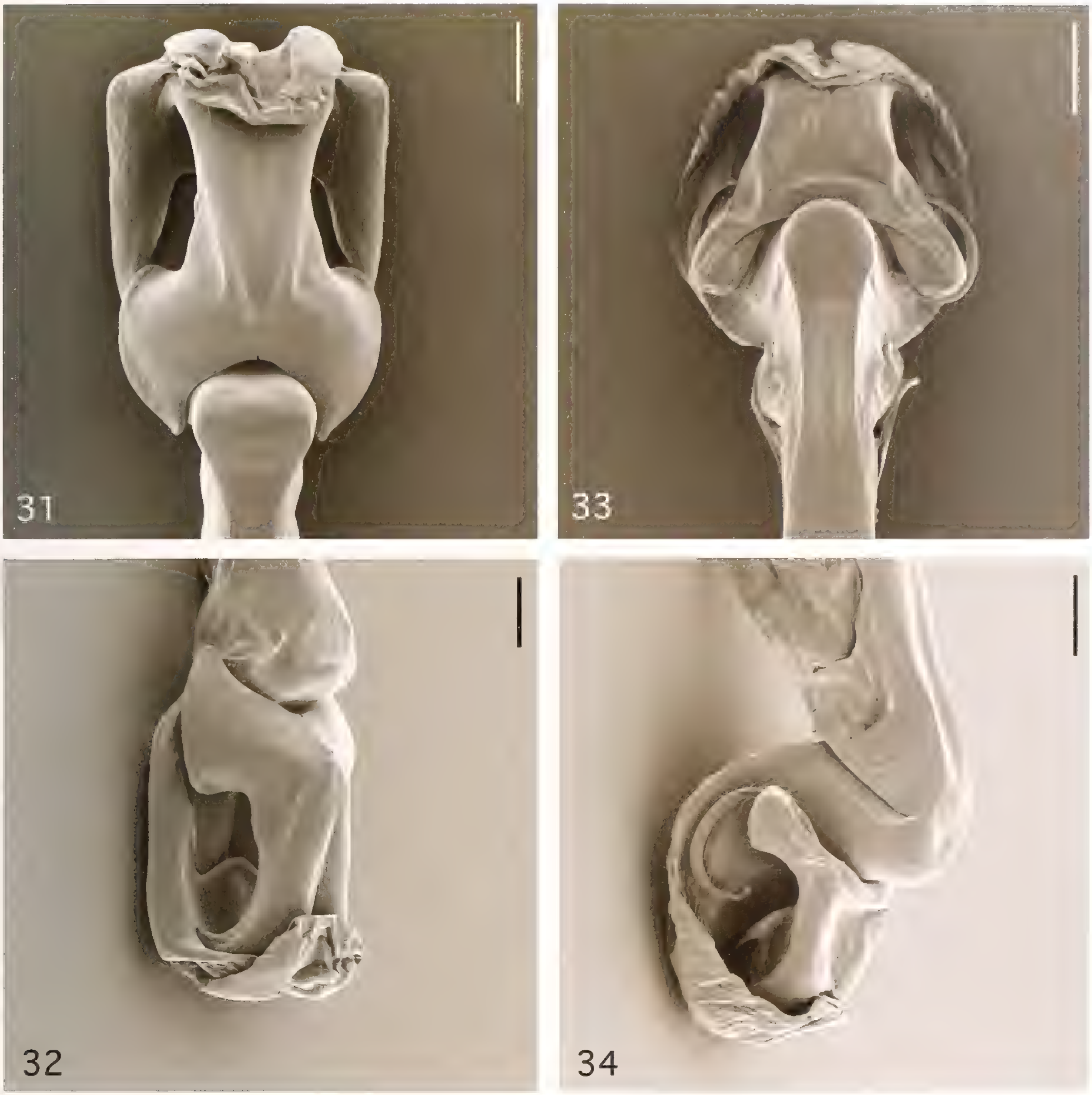
Figs. 19-22: Ligulae of ♂♂ in ventral (19, 21) and lateral view (20, 22): 19-20, *Leptocnemis cyanops*; 21-22, *Lochmaeocnemis malacodora*. Scale bars 100 µm.



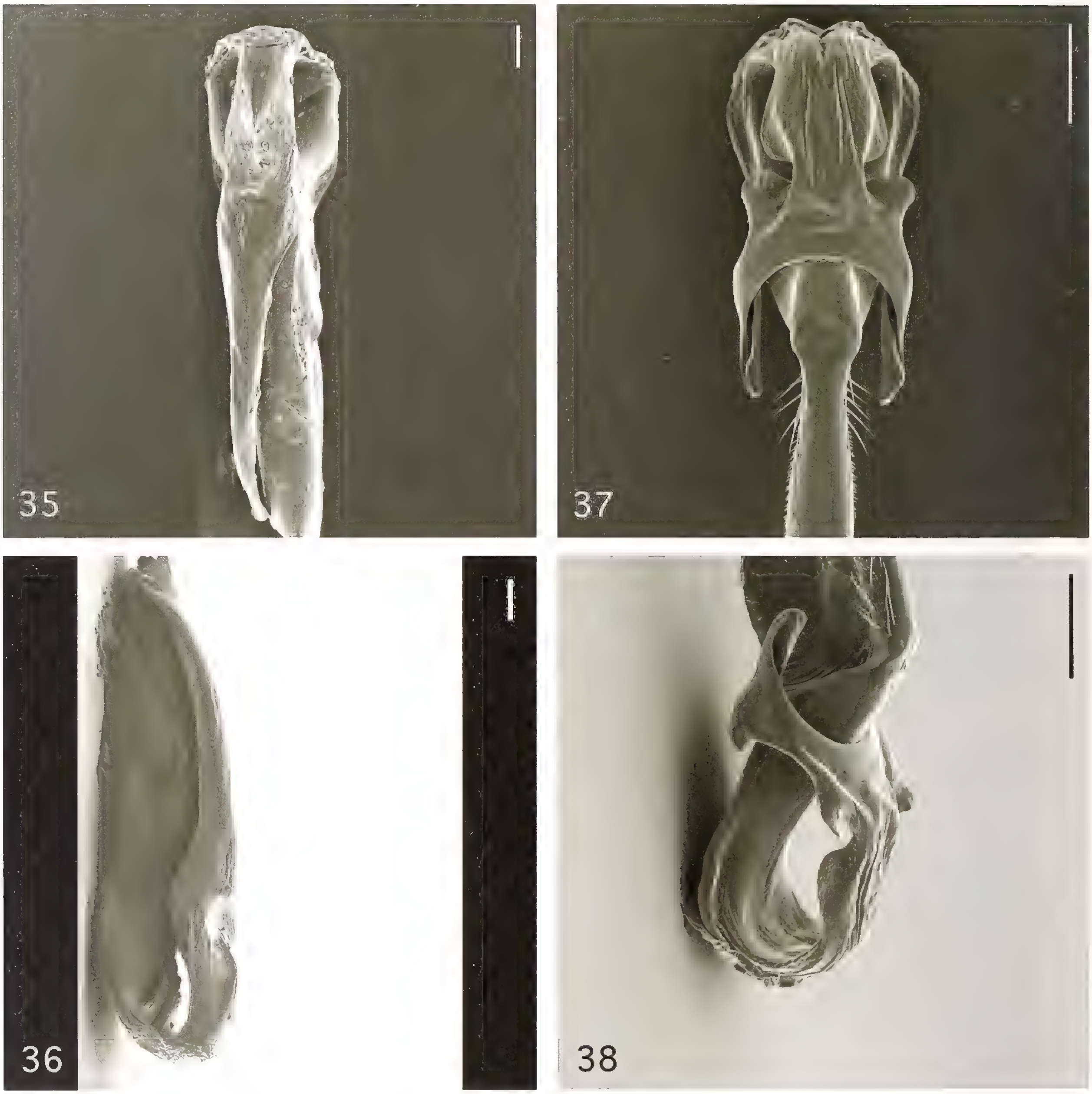
Figs. 23-26: Ligulae of ♂♂ in ventral (23, 25) and lateral view (24, 26): 23-24, *Mesocnemis singularis*; 25-26, *Paramecocnemis erythrostigma*. Scale bars 100 µm.



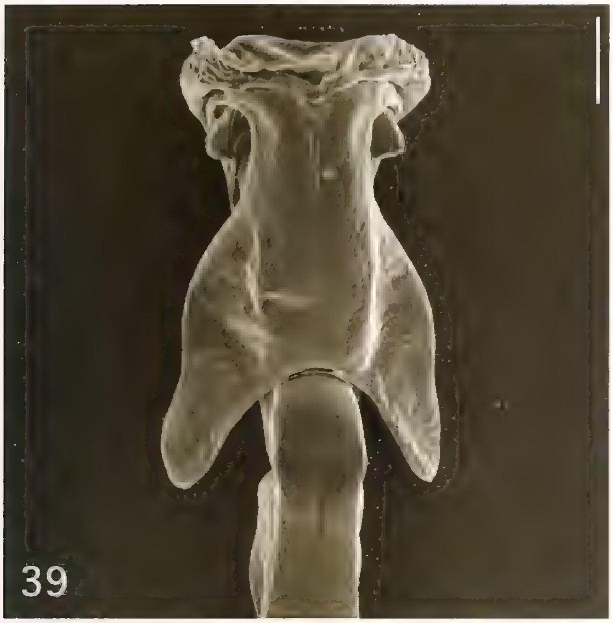
Figs. 27-30: Ligulae of ♂♂ in ventral (27, 29) and lateral view (28, 30): 27-28, *Rhyacocnemis leonorae*; 29-30, *Risiocnemis atropurpurea*. Scale bars 100 µm.



Figs. 31-34: Ligulae of ♂♂ in ventral (31, 33) and lateral view (32, 34): 31-32, *Risiocnemis appendiculata*; 33-34, *Risiocnemis gracilis*. Scale bars 100 µm.



Figs. 35-38: Ligulae of ♂♂ in ventral (35, 37) and lateral view (36, 38): 35-36, *Stenocnemis pachystigma*; 37-38, *Thaumatagrion funereum*. Scale bars 100 µm.



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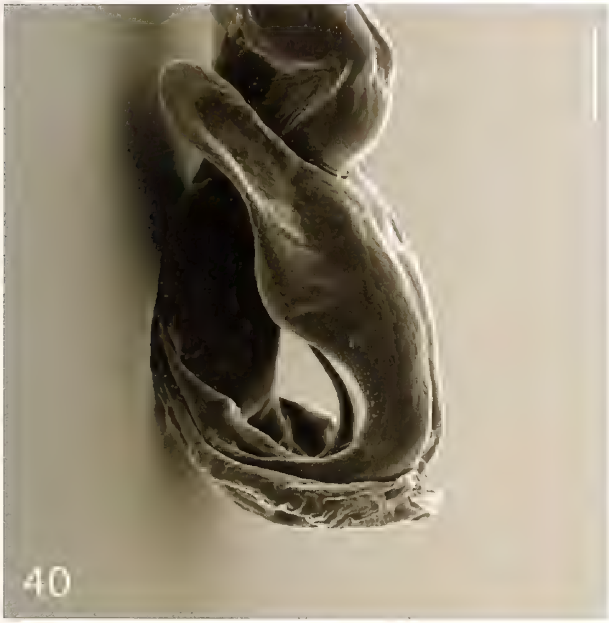


40

Figs. 39-40: Ligulae of ♂♂ in ventral (39) and lateral view (40): 39-40, *Torrenticnemis filicornis*, Scale bars 100 µm.

In the taxa concerned, the caudal end of abdomen is inflating dorsoventrally and/or laterally from segment 7 or segment 8 onwards.

55. Length ratio abdomen/hindwing.

(0) 1.4 ; (1) 1.5; (2) 1.6; (3) 1.7; (4) 1.8; (5) 1.9; (6) 2.1.

The length ratio of wing length and abdomen length is considerably constant within species; in cases where some variation occured, mean values were calculated.

Anal appendages

56. Length ratio inferior/superior anal appendages.

(0) about 3.0 times; (1) about 1.5 times; (2) 0.9 to 1.0 times; (3) 0.7 to 0.8 times; (4) 0.5 to 0.6 times; (5) 0.3 to 0.4 times; (6) 0.1 to 0.2 times.

For measuring the length of both inferior and superior appendages, curvation of appendages was taken into account as far as possible.

57. Length ratio superior appendages/abdominal segment 10.

(0) about half the length; (1) subequal; (2) about 1.3 times the length; (3) about 1.5 times the length; (4) about 1.75 times the length; (5) twice the length; (6) about 3 times the length.

To avoid measurement errors, the character states were only scored for those species with straight superior appendages.

58. Subbasal process.

(0) absent; (1) present.

In most of the taxa studied, there is a process situated more or less close to the base of superior appendage (Figs. 41-42, 44-45); it varies considerably in shape and length among the species (see below).

59. Subbasal process: shape.

(0) elongate, slender; (1) blunt, subtriangular; (2) acute, short; (3) hook-like, short; (4) long, flattened; (5) broad, flattened; (6) robust, rounded (Figs. 44-45); (7) protruding into a large extension; (8) short, slender; (9) notched squarish process; (10) broadly rounded.

60. Subbasal process: length.

(0) long; (1) of medium length; (2) short.

This character and the next were scored for Risiocnemis (Igneocnemis) species only because of both their good recognizability and discriminatory value in those species.

61. Subbasal process: position (in lateral view).

(0) Partly covered by posterior margin of abdominal segment 10 (in lateral view); (1) just distal to posterior margin; (2) moved further distally.

62. Inner median process.

(0) absent; (1) present.

The superior appendage of four species of the *Idiocnemis bidentata* species-group is furnished with an inner median process which is situated between subbasal and subdistal process; in *Idiocnemis bidentata*, the median process is almost fused with the subdistal one (cf. GASSMANN 2000: figs. 14-17).

63. Inner subdistal process.

(0) absent (Figs. 44-45); (1) small hook; (2) small tubercle; (3) finger-shaped hook; (4) slender hook; (5) blunt medium-sized hook; (6) tubercular protuberance, directed inwards; (7) subtriangular, hooked (Figs. 41-42); (8) large bulge.

64. Subdistal process: base.

(0) not prolonged; (1) moderately prolonged; (2) extensively prolonged.

In some (mainly *Lieftinckia*) species, the base of the subdistal process (hook) is considerably prolonged. Alternatively, the resulting elongate protuberance could also be interpreted and thus homologized as a distally moved subbasal process. However, its specific quality and position renders this alternative less plausible.

65. Superior appendage: second minute spine proximal to subdistal process.

(0) absent; (1) present.

66. Superior appendage: additional spines.

(0) absent; (1) present.

With an additional inner dorsal spine and a second inner baso-ventral spine, the superior appendage of *Lochmaeocnemis malacodora* is of far more complex built than that of other Calicnemiinae.

67. Superior appendage: curvature in lateral view.

(0) curved somewhat dorsad; (1) more or less straight; (2) only apically curved downwards; (3) sickle-shaped; (4) halfway incurved to right angle.

68. Superior appendage: curvature in dorsal view.

(0) apically incurved, tips converging; (1) sickle-shaped; (2) moderately incurved; (3) slightly incurved; (4) more or less straight.

69. Superior appendage: shape inner side (in dorsal view).

(0) halfway kinked outwards; (1) base bulgy, otherwise convex; (2) bulged out; (3) more or less straight; (4) only apically convex; (5) no such modifications.

70. Superior appendage: shape outer side (in dorsal view).

(0) slightly concave, kinked; (1) slightly convex; (2) bulged out; (3) more or less straight; (4) straight, distal part bent outwards; (5) no such modifications.

71. Superior appendage: shape of apex.

(0) rounded; (1) broadly rounded, somewhat flattened (Figs. 41-43; 44-46); (2) sharp; (3) complex, with inner plate; (4) notched; (5) subquadrangular.

72. Inferior appendage: shape in lateral view.

(0) straight, or slightly curved up; (1) strongly curved dorsad; (2) nearly plate-like, straight.

73. Inferior appendage: shape of apex.

(0) distinctly kinked inwards (Figs. 41-43); (1) slightly bent inwards; (2) not kinked inwards (Figs. 44-46).

In *Coeliccia membranipes* and *Indocnemis orang*, the apex of inferior appendage is distinctly kinked inwards as well as slightly bent downwards. *Calicnemia eximia* and *Allocnemis leucosticta* show the same feature, but less distinct.

74. Superior appendages: colour.

(0) black; (1) mainly black, with some yellow areas; (2) reddish; (3) reddish-brown; (4) yellow-brown; (5) yellow-orange; (6) yellow-white; (7) blue.

Ligula

75. Ligula: lateral hooks (cf. GASSMANN 2000).

(0) absent; (1) present (Fig. 12).

Cyanocnemis aureofrons and the species of the *Idiocnemis bidentata* - group exhibit more or less distinct lateral emarginations at the ligula head.

76. Ligula: distal median cleft (cf. GASSMANN 1999).

(0) absent; (1) present; (2) only slightly developed.

77. Ligula: flagella at ligula head.

(0) present (Figs. 5-6, 7-8, 17-18, 23-24, 33-34); (1) absent.

78. Ligula: terminal lobes.

(0) long, broad, apically subrectangular (Figs. 13-14); (1) of median length and width (Figs. 33-34, 39-40); (2) reduced (Figs. 11-12); (3) short, spatulate (Figs.15-16; Figs. 31-32); (4) long, broad, apically rounded; (5) long, very broad (Figs. 29-30); (6) very long, semi-acute (Figs. 35-36); (7) long, broad, apically hooked (Figs.19-20); (8) broad, of median length, subrectangular (Figs. 25-26, 27-28); (9) leaf-shaped, of median length (Figs. 21-22); (10) very broad, of median length; (11) very long, slender.

79. Ligula head: degree of folding.

(0) not folded; (1) slightly folded; (2) moderately folded; (3) strongly folded.

80. Ligula head: width.

(0) broad (Figs. 7-8, 15-16, 31-32, 33-34); (1) elongate, narrow (Figs. 13-14); (2) stout, as wide as long (Figs. 29-30); (3) elongate, subtriangular, widening distally.

81. Ligula: medio-lateral protrusion.

(0) absent; (1) present (Figs. 8, 28, 40).

82. Ligula head: inner protrusion.

(0) absent; (1) present (Figs. 4, 22, 28).

83. Ligula: apical ridge/plate.

(0) absent; (1) intermediate ridge (Figs. 15-16); (2) ridge (Figs. 33-34); (3) plate (Figs. 7-8).

84. Ligula: inner lamina/flagellum.

(0) lamina; (1) intermediate between lamina and flagellum (Fig. 16); (2) flagellum (Figs. 22, 40); (3) reduced to short process.

85. Ligula: incision between terminal lobes: shape.

(0) rounded (Figs. 5-6, 11-12, 13-14, 15-16, 17-18, 19-20, 21-22, 25-26, 27-28, 31-32, 33-34, 39-40); (1) arc-shaped; (2) slightly arc-shaped (Figs. 29-30); (3) sharp; (4) very sharp (Figs. 7-8, 23-24); (5) straight.

Female characters:

86. Female pronotal tubercles.

(0) distinct, high (Fig. 50); (1) distinct, of moderate height; (2) only sightly raised (Fig. 48), or bulgy.

The female pronotal tubercles can be flat up to slightly raised (Fig. 48), or extended into high conical processes (Fig. 50) which are mostly pointed apically.

87. Female posterior pronotal lobe.

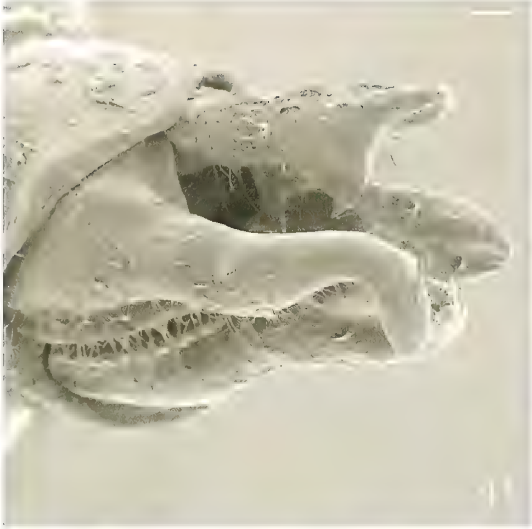
(0) trilobate; (1) undivided.

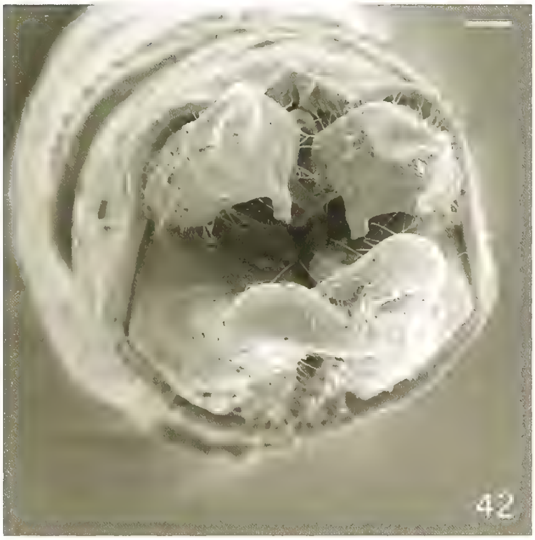
All species of genus *Risiocnemis* have the posterior pronotal lobe divided into a broad median lobe and a pair of narrow lateral lobes (Fig. 49). However, the character state 'trilobate' also circumscribes a condition where either the median lobe is completely lost or at least distinctly reduced.

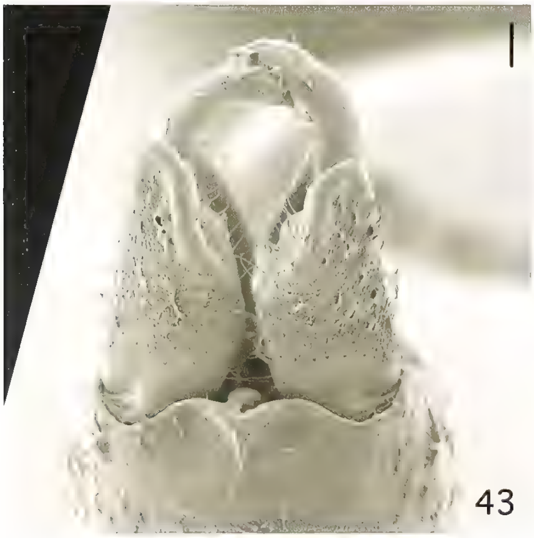
88. Female posterior pronotal lobe: elevation.

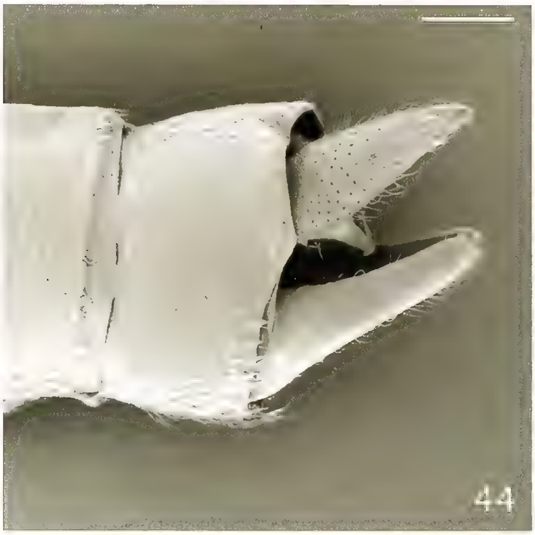
(0) directed anteriorly; (1) strongly elevated; (2) distinctly elevated (Fig. 50); (3) halfway elevated; (4) not or only slightly elevated (Fig. 48).

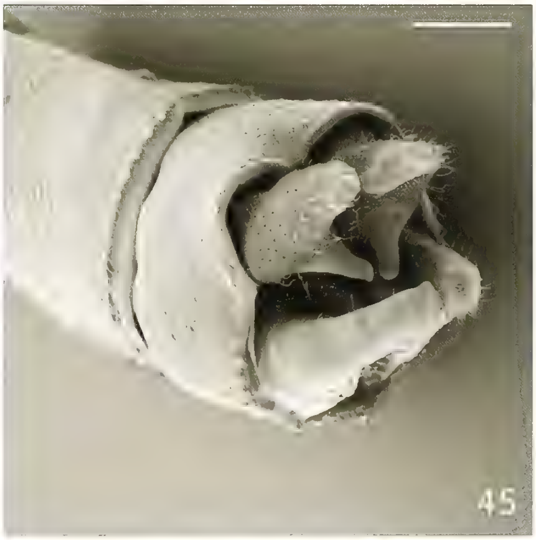
In case of species with trilobate posterior pronotal lobe, only the elevation of the median part (lobe) was determined.

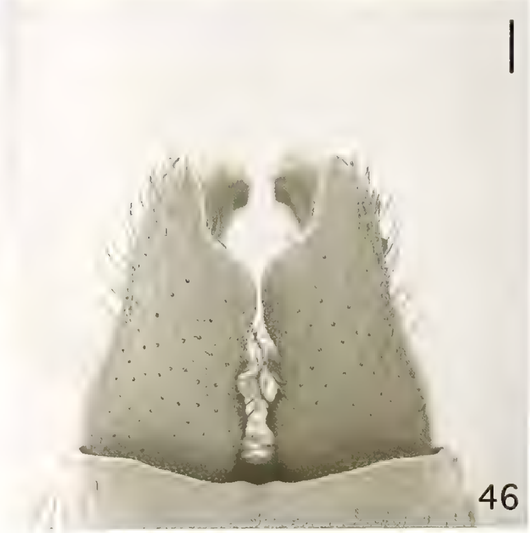




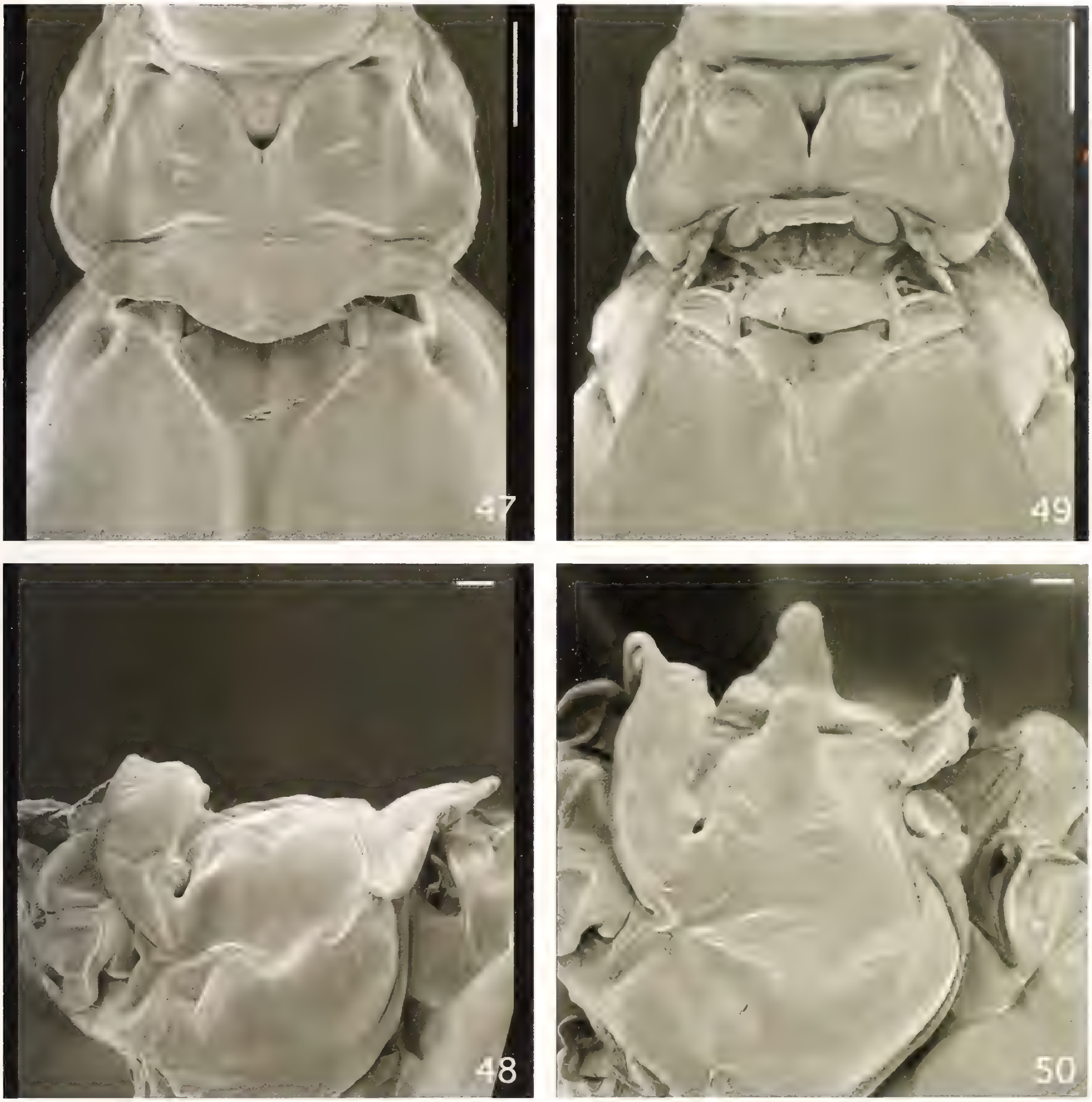








Figs. 41-43: Anal appendages of *Coeliccia membranipes*, ♂, in lateral (41), posterior (42) and dorsal (43) view. **Figs. 44-46:** Anal appendages of *Risiocnemis elegans*, ♂, in lateral (44), posterior lateral (45) and dorsal (46) view. Scale bars 300 µm (44, 45), 100 µm (41-43, 46).



Figs. 47-50: Prothorax of *Idiocnemis mertoni*, ♀ (47, 48) and *Risiocnemis elegans*, ♀ (49, 50) in dorsal (47, 49) and lateral (48, 50) view. Scale bars 300 µm (47, 49), 100 µm (48, 50).

3. RESULTS

3.1. Monophyly of Platycnemididae and Calicnemiinae

Within the scope of the present study, it was not possible to thoroughly test the hypothesis of monophyly for the family Platycnemididae and/or the subfamily Calicnemiinae; several families of Coenagrionoidea and even other superfamilies would have to be included in such an analysis. However, the morphological studies revealed putative synapomorphies which apparently have not been mentioned by other authors, and which could, however, be considered in future studies of higher-level phylogeny. For the Platycnemididae these are the only moderately kinked arculus (which is not nearly right-angled, as in at least some coenagrionides), and the comparatively long legs (femora of hind legs distinctly reaching beyond posterior margin of synthorax). In the present analysis, the Calicnemiinae turn out to be monophyletic with regard to the Platycnemidinae (*Copera* and *Platycnemis*); however, all apomorphic character states at the ingroup node experience one or more subsequent reversals or transformations in the ingroup; thus, there is no synapomorphy uniting all calicnemiines based on the present data set.

3.2. Phylogeny

The parsimony analysis resulted in 732 equally parsimonious cladograms (721 steps; consistency index: 0.406, retention index: 0.717, rescaled c.i.: 0.292), of which the strict consensus is shown in Figure 51. The strict consensus cladogram is largely resolved at the species level for the New Guinean *Idiocnemis* and the Philippine *Risiocnemis*. The monophyly of both genera as well as that of the smaller Papuan genera *Arrhenocnemis* and *Paramecocnemis* is confirmed. *Rhyacocnemis* forms a monophyletic group together with *Idiocnemis leonorae* which therefore is transferred to that genus (see below). The three representative species of the Oriental genera *Calicnemia, Coeliccia* (*C. membranipes*, Plate 1a) and *Indocnemis* also cluster together in the strict consensus. At the base of the cladogram, we find an unresolved assemblage consisting of all Afrotropical genera examined. The ingroup node is well supported (d=3). We find *Arrhenocnemis* (New Guinea) in a reasonably well supported but unresolved clade (d=2) together with the genera *Risiocnemis* (Philippines), and single species of *Lieftinckia* and *Salomocnemis* (Solomon Islands); at a higher level, this clade is part of a polytomy comprising *Asthenocnemis*, the smaller Papuan genera and the *Idiocnemis* clade. At the next higher level, the African taxa join into a polytomy also involving the *Coeliccia-/Indocnemis-/Calicnemia* - clade.

Idiocnemis Selys

The relationships among the *Idiocnemis* species turn out to be nearly fully resolved in the strict consensus cladogram. The *I. inornata* species-group (GASSMANN 1999) is monophyletic, leaving the *I. bidentata* - group (GASSMANN 2000) paraphyletic. The latter one shows a largely pectinate topology except for the two sister species *I. inaequidens* Lieftinck (Plate 1d) and *I. pruinescens*. Not surprisingly, *I. dagnyae* represents the "link" between the two species-groups; this species combines traits of both species-groups. The *I. inornata* - group is well supported (d=3); its subclades only partly reflect the preliminary subgroupings recognized by GASSMANN (1999): leaving aside group I which only consists of one single species, *I. inornata*, we find that group II (northern New Guinea) is distributed across two clades which are, however, not sister clades. Instead, most members of group III (eastern Papuan archipelagos) are united with the western representatives of the northern New Guinea species in one clade, while the northeastern New Guinea species, together with a single southern species, *I. australis* Gassmann (Plate 1c), are the sister group to the remaining clade.

Risiocnemis Cowley

The Philippine genus *Risiocnemis* as well as both of its subgenera turn out to be monophyletic. While subgenus *Risiocnemis* is reasonably well supported (d=2), the basal node of subgenus *Igneocnemis* is even more strongly supported with the highest decay index (d=5) of all clades. Within subgenus *Risiocnemis*, the mainly northern Philippine *R. serrata* - species-group (Plate 1f: *R. serrata*) is well supported (d=3). The sister group relationship of *R. rolandmuelleri* and *R. seidenschwarzi*, distributed in the West Visayans, is confirmed and thus the monophyly of the *R. rolandmuelleri* - species-group, although only weakly supported (d=1). Independent from the still uncertain position of *R. erythrura* and *R. praeusta*, the predominantly southernly distributed *R. appendiculata* - group can be considered clearly paraphyletic, with *R. kiautai* representing the sister taxon of the *R. serrata* - group, and *R. confusa* being the sister taxon of the *R. rolandmuelleri* - group. *R. arator*, the only representative of the fourth species-group defined by HÄMÄLÄINEN (1991a), is the most basal taxon of the group.

In subgenus *Igneocnemis*, *R. atripes* is the most basal species, followed by *R. rubricercus*; both species are from Mindanao. Proceeding further on, we find two distinct clades which are each, however, weakly supported (d=1). The first one comprises only species from the eastern Philippines (e.g. *R. kaiseri*, Plate 1e), except for *R. fuligifrons* which is distributed across northwestern Mindanao (Zamboanga Peninsula). The second one mainly contains a mixed assemblage of species from Mindanao and Luzon, but also from the West and East Visayan islands. There is little hierarchical structure and only weak support within both these clades, except for the well supported sister group relationships of *R. calceata/R. siniae*, and *R. flammea/R. odobeni*.

3.3. Preferred phylogenetic hypothesis

A survey of all equally parsimonious cladograms revealed that there are two different positions *Asthenocnemis* takes: either basal to a clade containing all Papuan representatives, or just in between the Papuan taxa. Here, the latter alternative is considered less favourable, because it would mean that reversals in at least four important structural characters would have taken place in *Asthenocnemis*: from a denticulate wing margin back to a smooth one, the reversal from an inner flagellum to a lamina as well as the increase in postquadrilateral cells in both fore- and hindwing. If we filter the (resolved) trees showing *Asthenocnemis* in a basal position out of the entire set of trees, we obtain 70 trees which only differ in minor details of inner-generic relationships. To reconstruct character evolution, one tree out of this subset was chosen as the preferred phylogenetic hypothesis (Fig. 52). According to this clado-

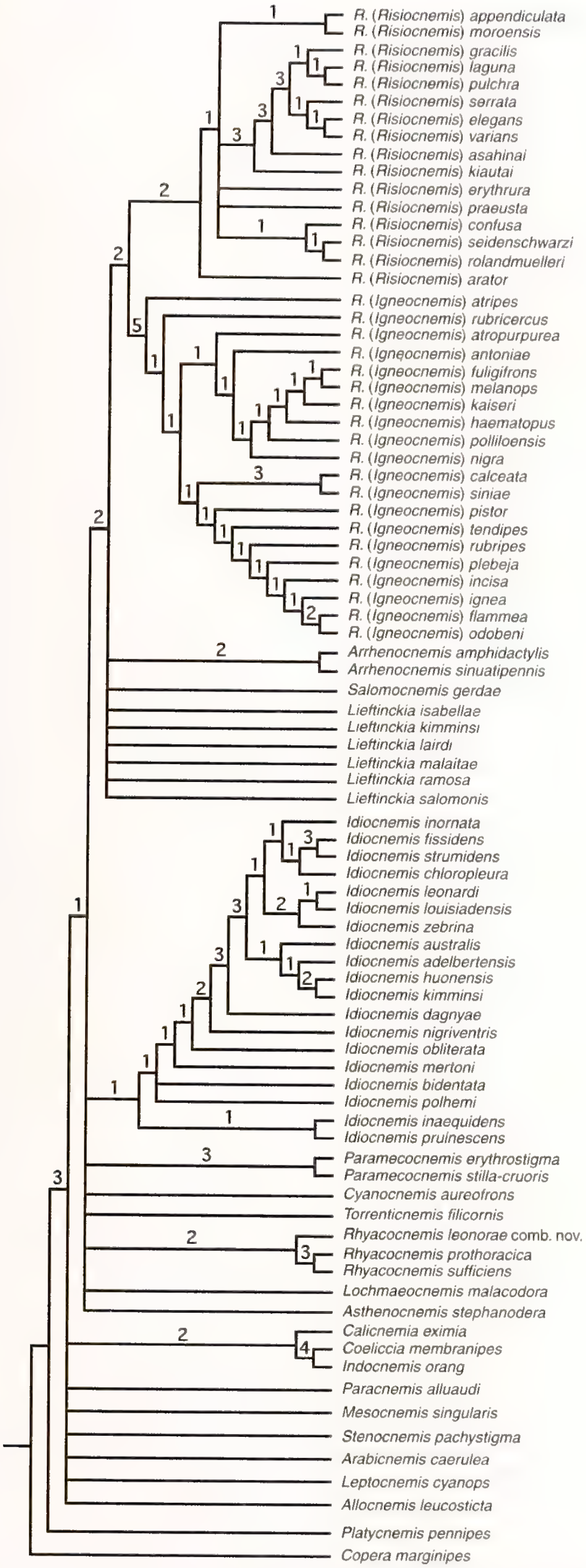
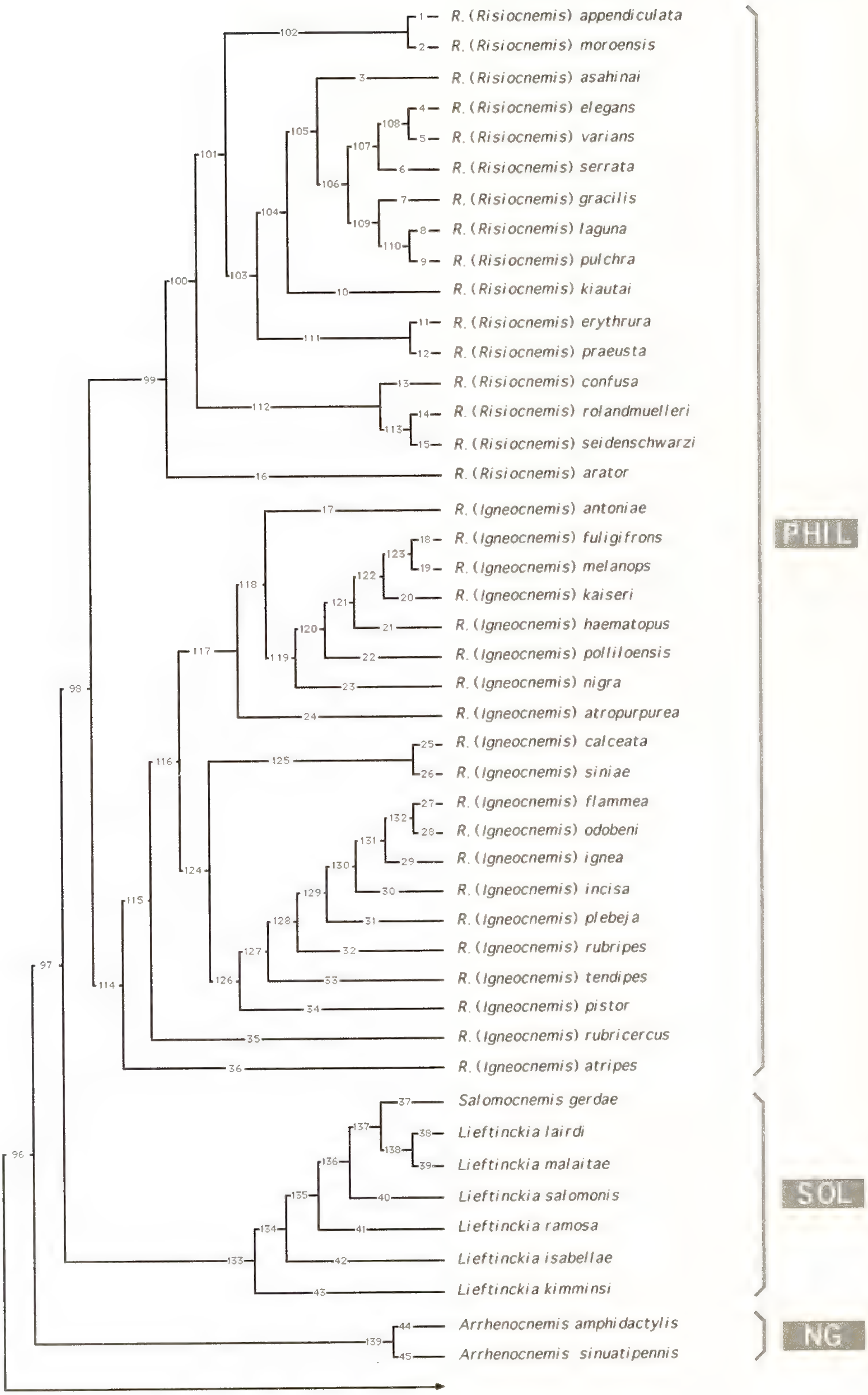

R. (Risiocnemis) appendiculata
R. (Risiocnemis) moroensis
R. (Risiocnemis) gracilis
R. (Risiocnemis) laguna
R. (Risiocnemis) pulchra
R. (Risiocnemis) serrata
R. (Risiocnemis) elegans
R. (Risiocnemis) varians
R. (Risiocnemis) asahinai
R. (Risiocnemis) kiautai
R. (Risiocnemis) erythrura
R. (Risiocnemis) praeusta
R. (Risiocnemis) confusa
R. (Risiocnemis) seidenschwarzi
R. (Risiocnemis) rolandmuelleri
R. (Risiocnemis) arator
R. (Igneocnemis) atripes
R. (Igneocnemis) rubricercus
R. (Igneocnemis) atropurpurea
R. (Igneocnemis) antoniae
R. (Igneocnemis) fuligifrons
R. (Igneocnemis) melanops
R. (Igneocnemis) kaiseri
R. (Igneocnemis) haematopus
R. (Igneocnemis) polilloensis
R. (Igneocnemis) nigra
R. (Igneocnemis) calceata
R. (Igneocnemis) siniae
R. (Igneocnemis) pistor
R. (Igneocnemis) tendipes
R. (Igneocnemis) rubripes
R. (Igneocnemis) plebeja
R. (Igneocnemis) incisa
R. (Igneocnemis) ignea
R. (Igneocnemis) flammea
R. (Igneocnemis) odobeni
Arrhenocnemis amphidactylis
Arrhenocnemis sinuatipennis
Salomocnemis gerdae
Lieftinckia isabellae
Lieftinckia kimminsi
Lieftinckia lairdi
Lieftinckia malaitae
Lieftinckia ramosa
Lieftinckia salomonis
Idiocnemis inornata
Idiocnemis fissidens
Idiocnemis strumidens
Idiocnemis chloropleura
Idiocnemis leonardi
Idiocnemis louisiadensis
Idiocnemis zebrina
Idiocnemis australis
Idiocnemis adelbertensis
Idiocnemis huonensis
Idiocnemis kimminsi
Idiocnemis dagnyae
Idiocnemis nigriventris
Idiocnemis obliterata
Idiocnemis mertoni
Idiocnemis bidentata
Idiocnemis polhemi
Idiocnemis inaequidens
Idiocnemis pruinescens
Paramecocnemis erythrostigma
Paramecocnemis stilla-cruoris
Cyanocnemis aureofrons
Torrenticnemis filicornis
Rhyacocnemis leonorae comb. nov.
Rhyacocnemis prothoracica
Rhyacocnemis sufficiens
Lochmaeocnemis malacodora
Asthenocnemis stephanodera
Calicnemia eximia
Coeliccia membranipes
Indocnemis orang
Paracnemis alluaudi
Mesocnemis singularis
Stenocnemis pachystigma
Arabicnemis caerulea
Leptocnemis cyanops
Allocnemis leucosticta
Platycnemis pennipes
Copera marginipes

Fig. 51: Strict consensus cladogram derived from all 732 equally parsimonious trees. Decay indices (Bremer support values) are indicated on the branches.


102
1 R. (Risiocnemis) appendiculata
2 R. (Risiocnemis) moroensis
3 R. (Risiocnemis) asahinai
4 R. (Risiocnemis) elegans
105
108
5 R. (Risiocnemis) varians
101
107
6 R. (Risiocnemis) serrata
106
7 R. (Risiocnemis) gracilis
104
109
8 R. (Risiocnemis) laguna
110
9 R. (Risiocnemis) pulchra
100
103
10 R. (Risiocnemis) kiautai
11 R. (Risiocnemis) erythrura
111
12 R. (Risiocnemis) praeusta
99
13 R. (Risiocnemis) confusa
112
14 R. (Risiocnemis) rolandmuelleri
113
15 R. (Risiocnemis) seidenschwarzi
16 R. (Risiocnemis) arator
17 R. (Igneocnemis) antoniae
18 R. (Igneocnemis) fuligifrons
123
19 R. (Igneocnemis) melanops
122
118
20 R. (Igneocnemis) kaiseri
121
120
21 R. (Igneocnemis) haematopus
117
119
22 R. (Igneocnemis) polliloensis
98
23 R. (Igneocnemis) nigra
24 R. (Igneocnemis) atropurpurea
25 R. (Igneocnemis) calceata
116
125
26 R. (Igneocnemis) siniae
27 R. (Igneocnemis) flammea
132
28 R. (Igneocnemis) odobeni
131
124
29 R. (Igneocnemis) ignea
130
115
30 R. (Igneocnemis) incisa
129
31 R. (Igneocnemis) plebeja
128
32 R. (Igneocnemis) rubripes
127
97
114
126
33 R. (Igneocnemis) tendipes
34 R. (Igneocnemis) pistor
35 R. (Igneocnemis) rubricercus
36 R. (Igneocnemis) atripes
PHIL
37 Salomocnemis gerdae
137
38 Lieftinckia lairdi
96
138
136
39 Lieftinckia malaitae
135
40 Lieftinckia salomonis
134
41 Lieftinckia ramosa
133
42 Lieftinckia isabellae
43 Lieftinckia kimminsi
SOL
44 Arrhenocnemis amphidactylis
139
45 Arrhenocnemis sinuatipennis
NG

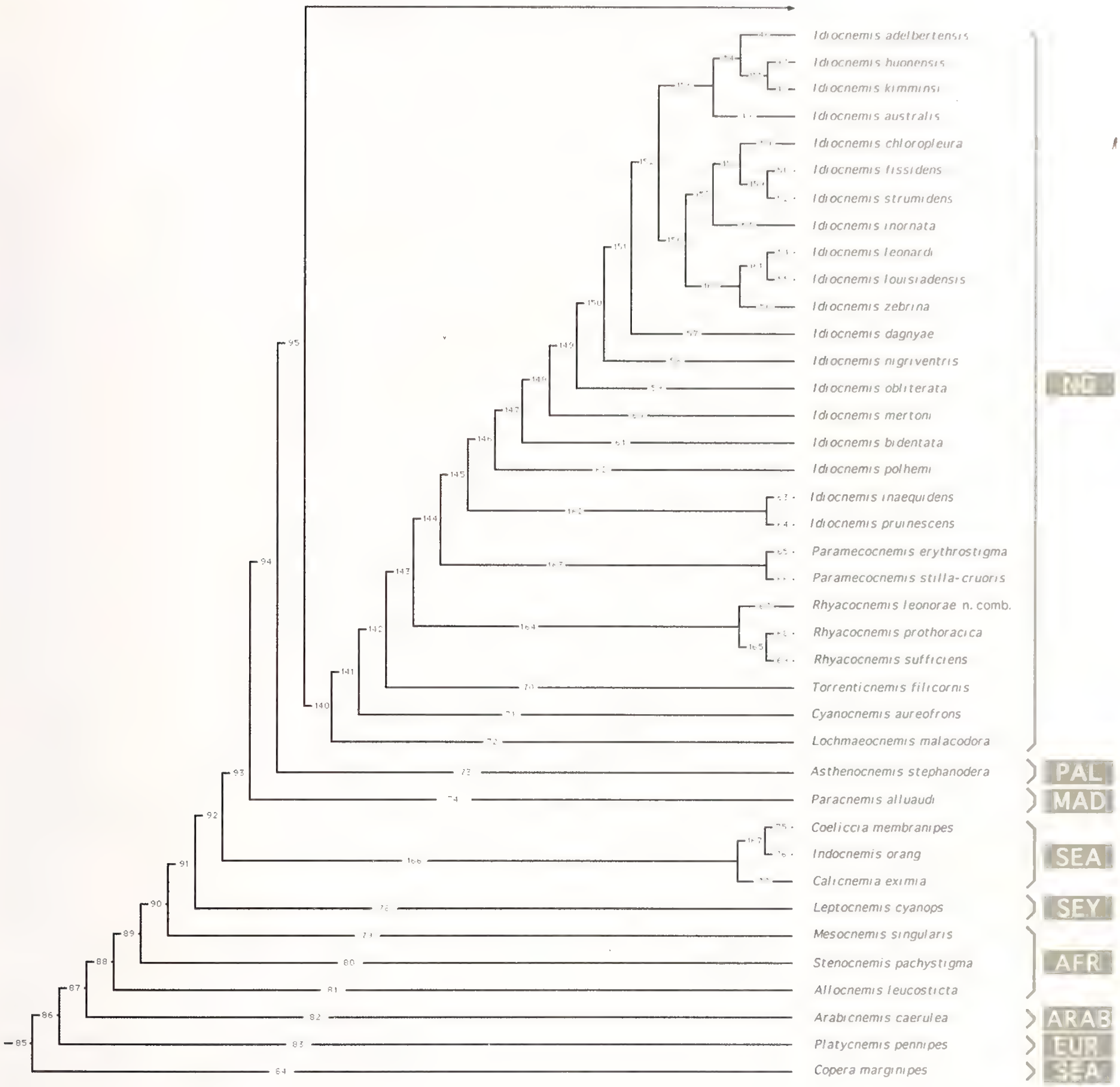

Idiocnemis adelbertensis
Idiocnemis huonensis
Idiocnemis kimminsi
Idiocnemis australis
Idiocnemis chloropleura
Idiocnemis fissidens
Idiocnemis strumidens
Idiocnemis inornata
Idiocnemis leonardi
Idiocnemis louisiadensis
Idiocnemis zebrina
Idiocnemis dagnyae
Idiocnemis nigriventris
Idiocnemis obliterata
Idiocnemis mertoni
Idiocnemis bidentata
Idiocnemis polhemi
Idiocnemis inaequidens
Idiocnemis pruinescens
Paramecocnemis erythrostigma
Paramecocnemis stilla-cruoris
Rhyacocnemis leonorae n. comb.
Rhyacocnemis prothoracica
Rhyacocnemis sufficiens
Torrenticnemis filicornis
Cyanocnemis aureofrons
Lochmaeocnemis malacodora
Asthenocnemis stephanodera
Paracnemis alluaudi
Coeliccia membranipes
Indocnemis orang
Calicnemia eximia
Leptocnemis cyanops
Mesocnemis singularis
Stenocnemis pachystigma
Allocnemis leucosticta
Arabicnemis caerulea
Platycnemis pennipes
Copera marginipes
NG
PAL
MAD
SEA
SEY
AFR
ARAB
EUR
SEA
85
86
87
88
89
90
91
92
93
94
95
140
141
142
143
144
145
146
147
148
149
150
151
164
165
166
80
81
82
83
84

Fig. 52: Preferred tree out of 70 equally parsimonious trees showing *Asthenocnemis* in comparatively basal position. Branch numbers refer to the character changes listed in Appendix 3. Paraphyly of the outgroup taxa is due to the rooting method. Abbreviations: AFR = Africa; ARAB = Arabian Peninsula; EUR = Europe; MAD = Madagascar; NG = New Guinea; PAL = Palawan; PHIL = Philippines; SEA = (Mainland) Southeast Asia, Sundaland; SEY = Seychelles; SOL = Solomon Islands.

gram, a sister group relationship between the Philippine *Risiocnemis* and the Solomon-clade (*Lieftinckia-Salomocnemis*) is proposed, based on two synapomorphies: the absence of an antehumeral stripe and the shape of the terminal abdominal segments which are not inflated. This clade shares two synapomorphies with its sister group, *Arrhenocnemis*: the reduction of postquadrilateral cells in forewing from three to just two, as well as the reduction of a dorsal marking on segment 9; furthermore, two characters change along branch 96: the colour of superior appendages (from black to yellow-brown; strongly homoplasious character), and the shape of the terminal lobes of the ligula (from the reduced state to short, spatulate lobes). At the next higher level, that clade described above is united with all Papuan taxa in a monophyletic group, resulting in an 'Indo-Pacific clade'; the latter comprises all Papuan and Philippine taxa and is characterized by the reduction of the third postquadrangular cell in the hindwing (synapomorphy of all representatives) as well as the absence of a transverse stripe on vertex (with a reduction to an only diffuse stripe in *Arrhenocnemis*). The most remarkable apomorphic trait of the 'Indo-Pacific clade', however, is the distinctly crenulate wing margin; however, it is reduced to a smoothly sinuous condition in *Igneocnemis*; thus, the distinctly crenulate wing margin turns out to be plesiomorphic in subgenus *Risiocnemis*. The New Guinean clade (excluding *Arrhenocnemis*) is characterized by an basal apomorphic change (branch 140) from an inner lamina to an inner flagellum of the ligula, however, it cannot be considered an autapomorphy of the whole clade because two independent subsequent reversals into an intermediate state take place, as well as one into a rudimentary short process. Five further character changes occur at the base of the New Guinea clade, but all of them experience subsequent reversals.

The large Indo-Pacific (sub)genera and their group-defining characters are as follows: *Igneocnemis* species firstly are characterized by the smoothly sinuous wing apex. Other synapomorphies of *Igneocnemis* species are the subequal length of antennal pedicellus and scapus, the pointed (sharp) apex of the superior appendage and the stout ligula head. Thus, in total, *Igneocnemis* species are united by four synapomorphies. Subgenus *Risiocnemis* is characterized by three synapomorphies, i.e. the distal position of the arculus, a slight brownish breath on wings as well as the trilobate female posterior pronotal lobe. A pair of brown spots lateral to the ocelli is an autapomorphy of the most recent common ancestor of sg. *Risiocnemis* and is maintained in all species except for *R. appendiculata*. Compared to *Risiocnemis* and its subgenera, the monophyly of *Idiocnemis* is weakly supported (see above). However, the genus is characterized by the following autapomorphies (= synapomorphies of its species): coloration of legs (light to medium brown, darkened to a varying extent) and the shape of the terminal abdominal segments (not or only slightly inflated).

3.4. Consequences for classification

Idiocnemis leonorae Lieftinck is transferred to *Rhyacocnemis* Lieftinck:

Rhyacocnemis leonorae (Lieftinck, 1956) **comb. nov.**

The genus now comprises three species, characterized by four synapomorphies, most of them referring to the peculiar shape of the male appendages: superior appendage apically incurved, with tips converging; inferior appendages rudimentary (0.1 to 0.2 times the length of superiors); apex of superior appendage sharp (homoplasious character). A distinct apomorphic trait of the ligula in *Rhyacocnemis* is the inner protrusion of the ligula head (Fig. 28); however, the condition in *R. prothoracica* is not known.

Since the position of *Salomocnemis* within one clade together with *Lieftinckia* (Fig. 52) is not stable (cf. consenus cladogram: Fig. 51), synonymization of the former genus with the latter is not considered here.

4. DISCUSSION

4.1. General

The present study should be considered a first approach to the phylogeny of Calicnemiinae. However, some conclusions can be drawn with relative certainty, i. e. the confirmed monophyly of the larger Indo-Pacific genera, especially *Risiocnemis*; there can also be no doubt about the monophyly of each of its subgenera. Unfortunately, basal relationships within Calicnemiinae are not unambigiously resolved, a fact which might be due to taxon sampling in the Oriental and African taxa, as well as to the fact that genera of doubtful family status (e.g. *Mesocnemis*) have been included; these factors potentially introduce homoplasy. Generally it holds that a large number of taxa keeps the consistency index low (KITCHING et al., 1998); with a taxa/character ratio of 84/88, the comparatively low actual c. i. (= 0.406) was to be expected. However, it was the intention of the author to include as many representatives of Calicnemiinae as possible to thoroughly cover the (morphological) diversity of the group. The monophyly of the subfamily Calicnemiinae in its present form remains doubtful; no unique synapomorphy for all species currently included has been found in the analysis with regard to Platycnemidinae; however, REHN (2003) found one synapomorphic trait supporting his *Coeliccia-Indocnemis/Risiocnemis* - clade: the absence of a large, proximal hornlike sclerite on the posterior articular plate. Unfortunately, this character could no longer considered (and examined) here after REHN's paper had come out. Although REHN's taxon sampling is rather scarce, certainly structural traits of the wing articulation appear to be important characters to continue with.

Possibly, there are indeed comparatively distinct morphological characters which allow for the assumption of monophyly at least for the family Platycnemididae: i.e. the characteristic course of the MA and IR3 veins. However, these characters are somewhat more difficult to examine in taxa with comparatively short wings. In REHN's study (2003) Platycnemididae is rendered paraphyletic, and the old world Protoneuridae form a monophyletic group together with the subfamily Platycnemidinae. Since REHN included only very few platycnemidid taxa, the significance of his findings has to remain open to further study. So, there have been indications for both the monophyly of Platycnemididae and Calicnemiinae, but also against it; apparently, only the monophyly of the subfamily Platycnemidinae has never been doubted. A detailed phylogenetic analysis of at least Coenagrionoidea, if possible including Lestoidea (Megapodagrionidae) is urgently required.

Although the present study was not designed to clarify the family status of dubiously assigned taxa, some notes might be appropriate. The genus *Arrhenocnemis* was included here because it shares the distinctly crenulate wing apex with all other Papuan Calicnemiinae (except *Thaumatagrion*, see below) and, in terms of wing venation, mediates between *Lieftinckia* and *Risiocnemis*. It is not clear to the author why LIEFTINCK (1971; short note in type catalogue) placed this genus in the Megapodagrionidae, although he originally described it as a "platycnemine" (LIEFTINCK 1933). In 1965, he wrote in his account on the Odonata of Madagascar, referring to the genus *Arrhenocnemis*: "... Like *Tatocnemis*, this was originally placed in Platycnemididae, but it is quite evident that both should be removed therefrom." Another doubtful case is the New Guinean *Thaumatagrion*: possibly Lieftinck had already something different in mind when he named the genus by using the suffix *-agrion* instead of *-cnemis*. In any case, he placed it within the Platycnemididae (LIEFTINCK 1932), a decision which is strongly questioned here. The general wing shape and colour, the size, but most of all, the largely zigzagged course of the MA and IR3 veins and the distinctly kinked arculus make the author consider it to be a potential coenagrionide; the 'very faintly denticulate margin' of the wing apex (LIEFTINCK 1932) differs considerably from that of the other Papuan taxa. Beside that, the ligula structure is different from all other known calicnemiine taxa: the presence of spines attached to the ligula shaft (Figs. 37-38) suggests a closer relationship with the Papuan coenagrionide genus *Oreagrion*. BECHLY (1996) considered the absence of those spines to be an autapomorphy of the family Platycnemididae. And, finally, no internal lamina or filament seems to be present (Fig. 38). Based on these considerations, *Thaumatagrion* was excluded from the present analysis. Since REHN's study, also the status of *Allocnemis* within the Platycnemididae is in question. In his analysis, this African genus turned out to be a sister group of a clade which contained the Calicnemiinae on one side and a clade consisting of Platycnemidinae and old world Protoneuridae on the other. As REHN points out himself, the sister group relationship between *Allocnemis* and Platycnemididae/Protoneuridae is based only on a single homoplasious character, the extension of the premental cleft (REHN 2003). In the present analysis, *Allocnemis*, clusters quite 'logically' between the African platycnemidides.

4.2. Relationships between calicnemiine genera

With regard to previous ideas on phylogenetic relationships within Calicnemiinae, both confirming and surprising results arose from the analysis. SCHMIDT suggested a close relationship between some Papuan genera (*Thaumatagrion, Paramecocnemis*) and the African *Mesocnemis* and *Metacnemis* (SCHMIDT 1951); these hypotheses are not at all corroborated by the present results. However, FRASER's suggestion of a close relationship between the Oriental genera *Calicnemia, Coeliccia* and *Indocnemis* has been confirmed (FRASER 1932). While LIEFTINCK (1963), in the light of the present analysis, was very right to consider *Lieftinckia* and *Risiocnemis* closely allied, he was apparently not with regard to *Idiocnemis* and *Coeliccia*. Some of these considerations were founded on larval morphology; however, LIEFTINCK himself stated that those findings are not always reliable because of the difficulties of assigning larval to adult stages in the field (LIEFTINCK 1984).

Remarkably, the Madagascan genera *Leptocnemis* and *Paracnemis* are found at slightly displaced positions within the cladogram (Fig. 52): instead of splitting off from the first, *Paracnemis alluaudi* branches off from the Oriental taxa. It should be noted that for *Paracnemis*, a total of 13 character states are either unknown to the author or - as those of the uniquely shaped male appendages - inapplicable and therefore coded as missing values in the data matrix. Thus, it is possible that the position of *Paracnemis* in the cladogram represents an artefact; this will be taken into account for biogeographic conclusions (VAN TOL & GASSMANN, in prep.).

The ambigious position of *Asthenocnemis stephanodera* in the set of equally parsimonious trees (see above) can possibly be explained by taxon sampling. Preliminary results from work on the *Coeliccia* species of the Greater Sunda Islands and the Philippines have revealed that *Asthenocnemis* probably just represents an 'offshot' of one of two monophyletic radiations within the genus *Coeliccia*, one of them partly leading to the colonization of geological terranes which today constitute the western and southern Philippines. In this context, *A. stephanodera* apparently is the most 'apomorphic' species (DIJKSTRA & GASSMANN, in prep.). Thus, it is very likely that insufficient taxon sampling is the cause for the unresolved position of *A. stephanodera* in the resulting set of cladograms since the mediating morphological traits are lacking. Consequently, further phylogenetic analyses of the Southeast Asian Calicnemiinae should include the highly interesting West Malesian radiations of *Coeliccia*. This would also contribute to the ongoing work on the historical biogeography of the group (GASSMANN, in prep.; VAN TOL & GASSMANN, submitted).

4.3. Perspectives for further studies of calicnemiine phylogeny

The present study has resulted in a first estimate of the phylogeny of the damselfly subfamily Calicnemiinae. It is apparent that basal relationships are still unsatisfactorily resolved (Fig. 51), and that the addition of taxa from the Oriental complex of genera (and the Palawan genus *Asthenocnemis* should be included in this context) is required. Firstly, this would allow for testing the uncertain monophyly of genera as *Calicnemia* and *Coeliccia*, which partly have been defined on the base of variable (polymorphic) wing venational traits of which the group-defining properties very much depend on our definition of the character states concerned. Secondly, it is necessary to newly define the generic borders between *Coeliccia* and *Asthenocnemis*. Several new as well as described species should be transferred to the latter genus; distinct putative synapomorphies have been found (DIJKSTRA & GASSMANN, in prep.). Thirdly, by increasing the range of taxa and of both morphological (e.g. endosceletal) and molecular characters, the ambigious phylogenetic position of *Asthenocnemis* could possibly be resolved.

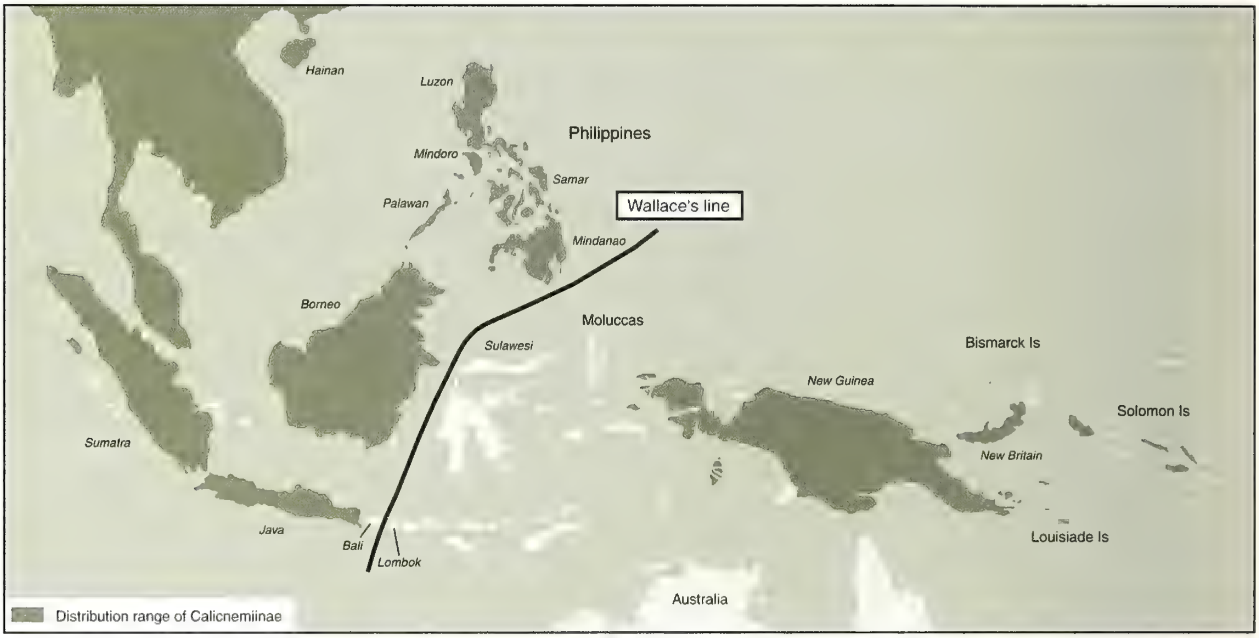


Fig. 53: Map of Malesia, with distribution range of Calicnemiinae indicated.

4.4. Implications for biogeography

As a group of insects occuring to the west and to the east of the Wallace line (Fig. 53), the Calicnemiinae are of special interest for biogeographical studies in the Indo-Australian transition zone. The phylogenetic hypothesis presented above allows for the postulation of active or passive dispersal events both into the East as well as, subsequently, back into the West (i.e. the Philippines). Since a detailed scenario for the distributional history of the group has been developed elsewhere in the context of the historical biogeography of the freshwater biota in Southeast Asia (VAN TOL & GASSMANN, submitted), the reader is referred to that forthcoming paper.

Acknowledgments. It is an honour to me to dedicate the present paper to the memory of Professor Clas M. Naumann (Zoological Research Institute and Museum Alexander Koenig Bonn, and University of Bonn/Germany), whom I owe a long lasting motivation and enthusiasm to work in the field of organismic biology; this as well as his support during the developing PhD thesis will be gratefully remembered. The present project is conducted under the direction of Prof. Dr. E. Gittenberger and J. van Tol (Leiden University and Natural History Museum, Leiden/Netherlands). I am grateful to Dr. H. Duffels (University of Amsterdam) for comments on the manuscript. I thank K.-D. Dijkstra (Leiden), Dr. M. Hämäläinen (Helsinki), Dr. A. Martens (Braunschweig) and Dr. J. Kuhn (Seewiesen) for information of different kinds, as well as Dr. H. Turner and C. Rüffler (Leiden) for general discussions. Most of curators and collection management staff of various collections I have either visited or received loans from have been acknowledged in previous papers. For additional specimens included here, I thank K.-D. Dijkstra, V. J. Kalkman (Leiden), Dr. W. Schneider (Hessisches Landesmuseum, Darmstadt) and Dr. G. Vick (Basingstoke, UK). I am grateful to Mrs. G. Lamers and Dr. W. de Priester (Institute of Biology, Leiden) for their permission to let me do my SEM studies; a minor part of the micrographs, however, has been made at the Natural History Museum Leiden, with thanks to J. Goud for assistance. Dr. John Michalski and Prof. Dennis Paulson (USA), Roland A. Müller (St. Gallen, Switzerland) and J. van Tol provided field photographs. For scanning of negatives and slides, I thank M. Brittijn and J. Meijvogel (IBL, Leiden).

Originally, the present research project was funded by the Dutch Life Science Foundation (ALW, formerly SLW), which is subsidized by the Netherlands Organisation for Scientific Research (NWO).

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APPENDIX 1

Taxa included in the cladistic analysis and their distribution
(m = male, f = female; [*] = only literature data available; [-] = not known).

Allocnemis Selys, 1863				
		Allocnemis leucosticta Selys, 1863	m/f*	Southern Africa
Arabicnemis Waterston, 1984				
		Arabicnemis caerulea Waterston, 1984	m/f*	Arabian Peninsula: Oman, Yemen
Asthenocnemis Lieftinck, 1949				
		Asthenocnemis stephanodera Lieftinck, 1949	m/f	Philippines: Palawan
Arrhenocnemis Lieftinck, 1933				
		Arrhenocnemis amphidactylis Lieftinck, 1949	m/-	Central northern New Guinea
		Arrhenocnemis sinuatipennis Lieftinck, 1933	m/-	Northern New Guinea
Calicnemia Strand, 1928				
		Calicnemia eximia (Selys, 1863)	m/f	Mainland southern/southeastern Asia, Hainan (first record), Taiwan
Coeliccia Kirby, 1890				
		Coeliccia membranipes (Rambur, 1842)	m/f	Greater Sunda Islands: Java, Sumatra
Copera Kirby, 1890				
		Copera marginipes (Rambur, 1842)	m/f	Southern and southeastern Asia
Cyanocnemis Lieftinck, 1949				
		Cyanocnemis aureofrons Lieftinck, 1949	m/f	Central northern New Guinea
Idiocnemis Selys, 1878				
	bidentata species-group			
		Idiocnemis bidentata Selys, 1878	m/f	Western New Guinea: Bird's Head Peninsula: Batanta; Salawati; Waigeo
		Idiocnemis dagnyae Lieftinck, 1958	m/f	Western New Guinea: Bird's Head Peninsula and southwestern New Guinea: Misool
		Idiocnemis inaequidens Lieftinck, 1932	m/f	Northeastern and eastern New Guinea
		Idiocnemis mertoni Ris, 1913	m/f	Southern New Guinea: Aru Islands

		Idiocnemis nigriventris Lieftinck, 1937	m/f	Northern New Guinea
		Idiocnemis obliterata Lieftinck, 1932	m/f	Northern and central northern New Guinea
		Idiocnemis polhemi Gassmann, 2000	m/f	Southeastern central New Guinea
		Idiocnemis pruinescens Lieftinck, 1937	m/f	Papuan Peninsula
	inornata species-group			
		Idiocnemis adelbertensis Gassmann, 1999	m/f	Northeastern New Guinea: Adelbert Range
		Idiocnemis australis Gassmann, 1999	m/f	Southern central and southern New Guinea
		Idiocnemis chloropleura Lieftinck, 1932	m/f	Northern New Guinea
		Idiocnemis fissidens Lieftinck, 1958	m/f	West Papuan Islands: Waigeo
		Idiocnemis huonensis Lieftinck, 1958	m/f	Northeastern New Guinea: Huon Peninsula
		Idiocnemis inornata Selys, 1878	m/f	Western New Guinea: Bird's Head Peninsula
		Idiocnemis kimminsi Lieftinck, 1958	m/f	Bismarck Archipelago: New Britain, Mioko
		Idiocnemis leonardi Lieftinck, 1958	m/-	Louisiade Archipelago: Tagula (Sudest)
		Idiocnemis louisiadensis Lieftinck, 1958	m/f	Louis. Arch.: Misima, Rossel; Marshall Bennett Arch.: Woodlark
		Idiocnemis strumidens Lieftinck, 1958	m/f	Western New Guinea: Bird's Head Peninsula and southwestern New Guinea; Misool
		Idiocnemis zebrina zebrina Lieftinck, 1958	m/f	Northeastern and central Papuan Peninsula
[excluded, see GASSMANN (2000)]				
		Idiocnemis leonorae Lieftinck, 1949	m/f	Northeastern and southern central New Guinea
Indocnemis Laidlaw, 1917				
		Indocnemis orang (Förster in Laidlaw, 1907)	m/f*	Southern and southeastern Asia
Leptocnemis Selys, 1886				
		Leptocnemis cyanops (Selys, 1869)	m/f*	Seychelles
Lieftinckia Kimmins, 1957				
		Lieftinckia isabellae Lieftinck, 1987	m/-	Solomon Islands: Santa Ysabel
		Lieftinckia kimminsi Lieftinck, 1963	m/f	Solomon Islands: Bougainville
		Lieftinckia lairdi	m*/f*	Solomon Islands: Guadalcanal

		Lieftinck, 1963		
		Lieftinckia malaitae Lieftinck, 1987	m/f	Solomon Islands: Malaita
		Lieftinckia ramosa Lieftinck, 1987	m/-	Solomon Islands: San Jorge; ? Bougainville
		Lieftinckia salomonis Kimmins, 1957	m/f	Solomon Islands: Guadalcanal
Lochmaeocnemis Lieftinck, 1949				
		Lochmaeocnemis malacodora Lieftinck, 1949	m/f	Central northern New Guinea
Mesocnemis Karsch, 1891				
		Mesocnemis singularis Karsch, 1891	m/f	Western Africa
Paracnemis Martin, 1903				
		Paracnemis alluaudi Martin, 1903	m/f	Madagascar
Paramecocnemis Lieftinck, 1932				
		Paramecocnemis erythrostigma Lieftinck, 1932	m/f*	Northern New Guinea
		Paramecocnemis stilla-cruoris Lieftinck, 1956	m*/-	Northeastern New Guinea
Platycnemis Burmeister, 1839				
		Platycnemis pennipes (Pallas, 1771)	m/f	Western and central Europe
Rhyacocnemis Lieftinck, 1956				
		Rhyacocnemis prothoracica Lieftinck, 1987	m*/-	Northeastern New Guinea
		Rhyacocnemis sufficiens Lieftinck, 1956	m/-	D'Entrecasteaux Islands: Goodenough
Risiocnemis Cowley, 1934				
	Subgenus *Risiocnemis* (*Risiocnemis*) Cowley			
		Risiocnemis appendiculata (Brauer, 1868)	m/f	Philippines: Mindanao; Dinagat; Camiguin; Samar; Leyte; Panaon; Biliran; Bohol; Homonhon
		Risiocnemis arator Hämäläinen, 1991	m/f	Philippines: northern/central Luzon
		Risiocnemis asahinai Kitagawa, 1990	m/f	Philippines: southern Luzon; Mindoro
		Risiocnemis confusa Hämäläinen, 1991	m/f*	Philippines: southern Luzon; Catanduanes
		Risiocnemis elegans Kitagawa, 1990	m/f	Philippines: Luzon

	Risiocnemis erythrura (Brauer, 1868)	m/f	Philippines: eastern Mindanao; Siargao
	Risiocnemis gracilis Hämäläinen, 1991	m/f	Philippines: central Luzon
	Risiocnemis kiautai Hämäläinen, 1991	m/f*	Philippines: Sibuyan
	Risiocnemis laguna Hämäläinen, 1991	m/f	Philippines: southern Luzon
	Risiocnemis moroensis Hämäläinen, 1991	m/f	Philippines: central Mindanao
	Risiocnemis praeusta Hämäläinen, 1991	m/f	Philippines: Dinagat; Samar; Leyte; Panaon; Biliran
	Risiocnemis pulchra Hämäläinen, 1991	m/f	Philippines: southern Luzon
	Risiocnemis rolandmuelleri Hämäläinen, 1991	m/f	Philippines: Sibuyan; Panay; Negros; Masbate; Siquijor
	Risiocnemis seidenschwarzi Hämäläinen, 2000	m/f*	Philippines: Cebu
	Risiocnemis serrata (Hagen in Selys, 1863)	m/f	Philippines: Luzon; Polillo; Marinduque; Catanduanes
	Risiocnemis varians Hämäläinen, 1991	m/f	Philippines: central northern Luzon.
Subgenus *Risiocnemis* (*Igneocnemis*) Hämäläinen			
	Risiocnemis antoniae Gassmann and Hämäläinen, 2002	m/f	Philippines: northeastern/eastern Mindanao
	Risiocnemis atripes (Needham and Gyger, 1941)	m/f	Philippines: central/eastern Mindanao
	Risiocnemis atropurpurea (Brauer, 1868)	m/f	Luzon; Marinduque
	Risiocnemis calceata Hämäläinen, 1991	m/f	Dinagat; Panaon
	Risiocnemis flammea (Selys, 1882)	m/f	Philippines: Mindanao; Dinagat; Biliran; Homonhon; Panaon; Leyte; Samar
	Risiocnemis fuligifrons Hämäläinen, 1991	m/f	Philippines: western/northern Mindanao; Dinagat; Basilan; Panaon; Leyte
	Risiocnemis haematopus (Selys, 1882)	m/f	Philippines: southern Luzon; Catanduanes
	Risiocnemis ignea (Brauer, 1868)	m/f	Philippines: northern/northeastern Luzon
	Risiocnemis incisa Kimmins, 1936	m/f	Philippines: northern and central Luzon
	Risiocnemis kaiseri Gassmann and Hämäläinen, 2002	m/f	Philippines: Samar
	Risiocnemis melanops Hämäläinen, 1991	m/f	Philippines: Samar
	Risiocnemis nigra	m/f	Philippines: Samar

	Gassmann and Hämäläinen, 2002		
	Risiocnemis odobeni Hämäläinen, 1991	m/f	Philippines: southeastern Luzon; Catanduanes
	Risiocnemis pistor Gassmann and Hämäläinen, 2002	m/-	Philippines: southeastern Mindanao
	Risiocnemis plebeja Hämäläinen, 1991	m/f	Philippines: Sibuyan; Panay
	Risiocnemis polilloensis Hämäläinen, 1991	m/f	Philippines: southeastern Luzon; Catanduanes; Polillo
	Risiocnemis rubricercus Gassmann and Hämäläinen, 2002	m/-	Philippines: eastern Mindanao
	Risiocnemis rubripes (Needham and Gyger, 1939)	m/f	Philippines: eastern Mindanao; Dinagat
	Risiocnemis siniae Hämäläinen, 1991	m/f	Philippines: Leyte; Samar
	Risiocnemis tendipes (Needham and Gyger, 1941)	m/f	Philippines: Mindanao
Salomocnemis Lieftinck, 1987			
	Salomocnemis gerdae Lieftinck, 1987	m/f	Solomon Islands: Guadalcanal
Stenocnemis Karsch, 1899			
	Stenocnemis pachystigma (Selys, 1886)	m/f	Western Africa
Torrenticnemis Lieftinck, 1949			
	Torrenticnemis filicornis Lieftinck, 1949	m/f	Central northern New Guinea

APPENDIX 2

Data matrix for the cladistic analysis of Calicnemiinae

	1	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778	88888888
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	12345678
Idiocnemis adelbertensis	2011400000	2200001355	321???0423	3200100221	0052100000	?00012?10?	?010002155	0025011101	00020218
Idiocnemis australis	2011400000	3200001355	321???0423	3200100221	0052100000	?00012?10?	?020002155	0025001200	00020219
Idiocnemis chloropleura	2011300000	2200001355	321???0423	3201101221	0072100000	?00013?10?	?010002155	0125011101	00020214
Idiocnemis fissidens	2011?00000	2200001355	??1????423	3201101221	0052101000	?00013?10?	?030002155	0025011133	000??219
Idiocnemis huonensis	2011400000	2200001355	321???0423	3202100221	0050?00000	?00012?10?	?010002255	0025011101	00020218
Idiocnemis inornata	2011300000	2200001355	321???0423	3201100221	0071200000	?00013?10?	?010002255	0025001401	0002021A
Idiocnemis kimminsi	2011400000	2200001355	321???0423	3202100221	0070?00000	?00012?10?	?010102255	0025011101	00020218
Idiocnemis leonardi	2011300000	4200001355	321???0423	3201100221	0070?01000	?00014?10?	?020002255	0025001201	00020???
Idiocnemis louisiadensis	2011300000	3200001355	321???0423	3201100221	0070?01000	?00012?10?	?020002255	0025001201	0002021C
Idiocnemis strumidens	2011300000	2200001355	321???0423	3201101221	0052100000	?00013?10?	?040002155	0025011133	000?0219
Idiocnemis zebrina	2011300000	3200001355	321???0423	3201100221	0070?01000	?00023?10?	?020002155	0025001300	0011021C
Idiocnemis bidentata	2011400000	22000013A0	3201040400	0223100021	0202300000	010013?11?	?150003155	0021101011	000?021B
Idiocnemis dagnyae	2011300000	2200001397	321???0423	32{02}0100221	0{01}72300000	010013?11?	?030003155	0025101011	000?021B
Idiocnemis inaequidens	2011300000	2200001000	1201040400	0223100021	0202300100	010014?12?	?050003255	0020101021	000?0210
Idiocnemis mertoni	2011300000	2200001334	3201040400	0223100021	0200?00000	010014?11?	?050003155	0025101011	000?021B
Idiocnemis nigriventris	2011300000	2200001363	32010?0403	0203100021	0212300000	010013?13?	?120003255	0025101021	000?0210
Idiocnemis obliterata	2011300000	2200001334	3201040400	0223100021	0212300000	010013?11?	?150003155	0025101011	000?0210
Idiocnemis polhemi	2011300000	2200001320	3201040401	1223100021	0202300000	010013?11?	?150003155	0020101011	000?0210
Idiocnemis pruinescens	2011300000	2200001040	3201040400	0223100021	0202300100	010023?10?	?050003255	0021101011	000?021D
Risiocnemis appendiculata	2011400000	4400011570	221???2423	2200100221	0070?0?000	?00022314?	?00?000255	0022001300	0000020?
Risiocnemis arator	2011400000	44000110B0	021????400	0300110021	0270?0?000	?00012114?	?00?001455	0020000?01	0000000?
Risiocnemis asahinai	2011400000	34000110C9	000101?400	0300110021	027201?000	?00023318?	?00?001455	0027000100	0020000?
Risiocnemis confusa	2021400000	4400011010	021????400	0300110021	0270?0?001	?00014113?	?00?001455	0022001300	0000020?
Risiocnemis elegans	2011400000	44000116C9	000011?400	0300111021	027201?000	011022116?	?00?001445	1027000100	0020000?
Risiocnemis erythrura	2011400000	44000111B0	021????400	0300110021	0270?0?001	?00032114?	?00?001455	0022001300	0000020?
Risiocnemis gracilis	2011400000	4400011123	101????400	0200110021	027202?000	011033110?	?00?001455	0027000100	0020000?
Risiocnemis kiautai	2011400000	44000116C9	800111?408	0300110021	0270?0?000	?00032114?	?00?001455	1027001300	0000020?
Risiocnemis aguna	2011400000	44000111C9	100111?400	0200110021	027201?000	011032118?	?060001445	0027000100	0020000?
Risiocnemis moroensis	2011400000	44000120B0	021????400	0200110021	0270?0?001	?00053314?	?00?001455	0023001300	0000020?
Risiocnemis praeusta	2011400000	44000110B0	021????400	0300110021	0270?0?001	?00032114?	?00?001455	1022001300	0000020?
Risiocnemis pulchra	2011400000	44000116C9	8001012400	0200110021	027202?000	011032118?	?060001445	0027000100	0020000?
Risiocnemis rolandmuelleri	2021400000	44000111B0	121????400	8300110021	027200?000	?00012113?	?00?001455	0020000300	0000020?
Risiocnemis seidenschwarzi	2021400000	44000110C0	021????400	030011?0?1	027200?000	?00024117?	?0??001455	002000030?	0000?20?
Risiocnemis serrata	2011400000	44000116C9	800011?400	0300111021	023201?000	011034113?	?00?001455	0027000100	0020000?
Risiocnemis varians	2011400000	44000110C9	000011?400	0300111021	027201?000	011022118?	?060001445	0027000100	0020000?
Risiocnemis antoniae	1011200000	4400001000	031????400	0000100071	0270?0?000	?000223100	100?001413	2022001502	0000021J
Risiocnemis atripes	1011200000	44000010B0	031????400	0000100001	0270?0?000	?000141151	000?001433	2021001502	0000021K
Risiocnemis atropurpurea	1011200000	4400001000	021????400	0000100080	0270?0?000	?000243162	000?001433	2021001502	0000221H
Risiocnemis calceata	1011200000	4400001000	031????400	{02}000100051	0270?0?001	?000233152	000?001434	2022001502	0000321J
Risiocnemis flammea	1011200000	4400001574	221???2425	5000100271	0070?0?000	?000343100	100?001400	2022001502	0000021E
Risiocnemis fuligifrons	1011200000	4400001070	031????420	2000100271	0070?0?000	?000345101	200?001411	2021001502	0000021H
Risiocnemis haematopus	1011200000	4400001000	031????400	0000100071	0270?0?000	?000343101	100?001411	2021001502	0000021H
Risiocnemis ignea	1011200000	4400001276	231???2422	2000100271	0070?0?000	?000255101	100?001433	2022001202	0000021H
Risiocnemis incisa	1011200000	4400001242	431???2422	2000100271	0070?0?000	?0002{34}3101	000?001433	2022001502	0000021J
Risiocnemis kaiseri	1011200000	4400001000	031????400	2000100041	0270?0?000	?000444101	100?001411	2021001502	0000021E

APPENDIX 2 (CONTINUED)

	1	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778	888888[illegible]
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	[illegible]
Risiocnemis melanops	1011200000	4400001042	031????400	2000100271	0070?0?000	?000343101	100?001411	2021001502	00000211
Risiocnemis nigra	1011200000	4400001000	021????400	0000100011	0270?0?000	?000343100	100?001400	2021001502	0000021[illegible]
Risiocnemis odobeni	1011200000	4400001{02}8{06}	{02}31???241{02}	{02}000100271	0070?0?001	?000245100	100?001400	2021001502	0000021[illegible]
Risiocnemis plebeja	1011200000	4400001542	331???2422	2000100271	0070?0?000	?000242102	000?001433	2024001502	00000217
Risiocnemis pistor	1011200000	4400001000	031????400	0000100271	0270?0?000	?000343152	100?001433	2022001502	0001[illegible]
Risiocnemis polliloensis	1011200000	4400001000	021????400	0000100041	0270?0?000	?000343101	100?001410	2021001502	00000211
Risiocnemis rubripes	1011200000	4400001245	231???2422	2000100271	0070?0?000	?000243152	100?001433	2022001502	00001211
Risiocnemis rubricercus	1011200000	4400001040	021????400	0000100001	0270?0?000	?000143152	000?001422	2022001502	0001[illegible]
Risiocnemis siniae	1011200000	4400001000	031????400	0000100051	0270?0?001	?000245152	000?001434	2022001502	0000321[illegible]
Risiocnemis tendipes	1011200000	4400001000	031????420	2000100271	0270?0?000	?000253152	000?001433	2022001502	00000217
Paramecocnemis erythrostigma	2011200000	2210001720	7201070400	0203101211	022200?000	010165?0??	?08?004255	3020001801	00020210
Paramecocnemis stilla-cruoris	2011200000	22100?1800	6?0107?400	0203101011	020260?000	?00164?0??	?08?004355	3020?0???1	????????
Cyanocnemis aureofrons	2001231110	0001021028	010205?404	0200100001	027200?000	010103?11?	?071002255	0020101201	00030210
Torrenticnemis filicornis	2001231000	0000031000	4201062400	0203100001	020240?010	01010260??	?00?002255	0020021101	10020211
Idiocnemis leonorae	2011230000	010000184B	6201032400	0203100?11	0062?0?000	010106?11?	?050001055	2??0001801	110?0212
Lochmaeocnemis malacodora	2001232000	0000031020	021????400	0300100001	0202?0?000	010103?10?	?040012255	2020001901	01020210
Arrhenocnemis amphidactylis	2001410000	24000018E0	6000061300	0300100021	120200?000	?00113?0??	?00?001255	0024??????	????????
Arrhenocnemis sinuatipennis	2001410000	4400001660	8?0001??26	3?03100?21	020200?000	?0011220??	?032001355	0024001301	000?0???
Rhyacocnemis prothoracica	2011220000	10000?1820	5200032400	0303100011	02??20?000	010116?11?	?00?002055	2020001?01	??020???
Rhyacocnemis sufficiens	2011220000	1000011820	5201032400	0300100011	0202?0?000	010116?11?	?00?002055	2??0001101	11020???
Salomocnemis gerdae	2011200000	02000018EB	621????4??	?000101??1	0?72?0?000	?00021411?	?00?001455	2025001301	00110?10
Lieftinckia isabellae	2031200000	2000011001	020000?400	?000100?21	007??0?000	?0001411A?	?011101255	0024?0???1	?0??????
Lieftinckia kimminsi	2031200000	2300001001	020001?400	0300100021	02???0?000	?00022119?	?012001355	0021001201	00010213
Lieftinckia lairdi	2031400000	22000?1???	??1????4?3	330010?121	00???0?000	?000?120??	?00?001455	0025001300	00110?13
Lieftinckia malaitae	20314?0000	2200001271	221???2423	3500100221	007??0?000	?0001120??	?00?001455	0021?01??1	?0???213
Lieftinckia ramosa	2031400000	2200011271	221????4{02}0	0100100221	00???0?000	?0002210??	?012001355	0024?01??1	?0??????
Lieftinckia salomonis	20314?0000	2200011276	2?1???24?3	?400100121	007??0?000	?00011110?	?00?001455	2024001301	00110213
Coeliccia membranipes	0011232020	11010010C0	821???2100	0300000021	020200?000	011021119?	?070001455	1007000?00	1030410?
Asthenocnemis stephanodera	0011222020	22000016C0	8200002006	6203102221	000200?000	01011260??	?08?001355	3020001201	0100?115
Calicnemia eximia	0001232010	0001001348	4202052004	4300000061	020240?000	?00011119?	?00?001455	0015000??1	00000214
Indocnemis orang	0001232221	0101003020	021????100	0300000001	020250?000	011011219?	?070001455	1000000??1	?0000214
Arabicnemis caerulea	0100030000	00000007DA	7?1???2437	7200100281	0000?0?000	?00023110?	?00?001455	2117001A01	0000010?
Leptocnemis cyanops	1011232020	0001011320	121????200	0200100021	0242?0?000	??1024?10?	?00?002255	2120001701	0000020?
Allocnemis leucosticta	0010220000	2201131820	6201021400	0500100011	020270?000	111021?19?	?00?001255	0015??1B01	000?020?
Mesocnemis singularis	0101032221	0000001?30	12??????00	0500100011	0???0?200	211005110?	?00?001455	2020000??1	?000420?
Paracnemis alluaudi	0000232120	00010016B0	8200011000	??00100081	0202?0?000	011012010?	?00?00??55	52?000??01	000?0210
Stenocnemis pachystigma	0001130000	00000013A8	421???2000	4300100011	020270?000	111012410?	?00?001455	2120001601	0000?214
Copera marginipes	0000400000	0000000450	721???2000	0100000030	020270?000	111040?0??	?00?00??55	0016001201	0000?116
Platycnemis pennipes	0000200000	000000145A	7201022000	0300001080	020250?000	11100110??	?00?001455	4007000??1	000?510?

APPENDIX 3

List of unambigious character state changes along branches of the preferred most parsimonious cladogram (cf. fig. 52).

Branch 1: char. 18: 0→5; char. 19: B→7; char. 21: 0→2; char. 29: 0→2; char. 30: 0→3; char. 31: 0→2; char. 36: 1→0; char. 38: 0→2; char. 42: 2→0; char. 67: 1→0; char. 68: 4→2. Branch 2: char. 17: 1→2; char. 50: 0→1; char. 56: 2→3; char. 74: 2→3. Branch 3: char. 11: 4→3; char. 55: 3→2; char. 56: 2→3; char. 57: 1→3. Branch 4: char. 59: 8→6; char. 71: 0→1; char. 88: 1→2. Branch 5: char. 63: 0→6. Branch 6: char. 21: 0→8; char. 43: 7→3; char. 56: 2→4; char. 59: 8→3; char. 88: 1→4. Branch 7: char. 19: C→2; char. 20: 9→3; char. 23: 0→1; char. 56: 2→3; char. 59: 8→0. Branch 8: none. Branch 9: char. 21: 1→8. Branch 10: char. 21: 0→8; char. 30: 0→8; char. 71: 0→1. Branch 11: char. 18: 0→1. Branch 12: char. 71: 0→1. Branch 13: char. 19: B→1; char. 50: 0→1. Branch 14: char. 18: 0→1; char. 21: 0→1; char. 31: 0→8. Branch 15: char. 19: B→C; char. 55: 1→2; char. 59: 3→7. Branch 16: char. 74: 2→0; char. 77: 1→0; char. 86: 2→0. Branch 17: char. 22: 2→3; char. 56: 4→2. Branch 18: char. 29: 0→2; char. 57: 3→5; char. 61: 1→2. Branch 19: char. 20: 0→2; char. 88: 1→2. Branch 20: char. 39: 7→4; char. 55: 3→4; char. 57: 3→4. Branch 21: none. Branch 22: char. 39: 7→4. Branch 23: char. 39: 7→1; char. 69: 1→0. Branch 24: char. 39: 7→8; char. 40: 1→0; char. 85: 0→2. Branch 25: char. 56: 4→3. Branch 26: char. 57: 3→5; char. 88: 4→3. Branch 27: char. 18: 2→5; char. 20: 6→4; char. 22: 3→2; char. 30: 2→5; char. 31: 2→5; char. 55: 2→3. Branch 28: char. 19: 7→8; char. 29: 2→1; char. 50: 0→1; char. 74: 2→1. Branch 29: char. 56: 4→5; char. 78: 6→2. Branch 30: char. 21: 2→4. Branch 31: char. 18: 2→5; char. 21: 2→3; char. 57: 3→2; char. 74: 2→4. Branch 32: char. 61: 0→1; char. 85: 0→1; char. 88: 4→1. Branch 33: char. 56: 4→5. Branch 34: char. 55: 2→3; char. 61: 0→1; char. 85: 0→1. Branch 35: char. 69: 3→2; char. 70: 3→2; char. 85: 0→1. Branch 36: char. 22: 2→3; char. 74: 2→1. Branch 37: char. 3: 3→1; char. 5: 4→2; char. 11: 2→0; char. 18: 2→8; char. 19: 7→E; char. 20: 1→B; char. 21: 2→6; char. 37: 0→1; char. 55: 1→2. Branch 38: char. 80: 1→0. Branch 39: char. 74: 5→1. Branch 40: char. 20: 1→6; char. 32: 0/3→4; char. 88: 4→3. Branch 41: char. 32: 0/3→1; char. 55: 1→2; char. 58: 1→0. Branch 42: char. 56: 2→4; char. 59: 0→A; char. 64: 2→1; char. 65: 0→1; char. 68: 3→2. Branch 43: char. 55: 1→2; char. 59: 0→9; char. 74: 4→1; char. 78: 3→2. Branch 44: char. 26: 1→6; char. 41: 0→1; char. 56: 2→3; char. 68: 3→2. Branch 45: char. 29: 0→2; char. 30: 0→6; char. 31: 0→3; char. 34: 0→3; char. 63: 0→3. Branch 46: none. Branch 47: none. Branch 48: char. 43: 5→7; char. 65: 0→1. Branch 49: char. 11: 2→3; char. 80: 1→0. Branch 50: char. 72: 0→1. Branch 51: char. 47: 0→1. Branch 52: none. Branch 53: char. 44: 2→1; char. 45: 1→2; char. 68: 1→2; char. 88: 4→1. Branch 54: char. 11: 3→4. Branch 55: none. Branch 56: char. 55: 1→2; char. 80: 1→0; char. 83: 0→1; char. 84: 2→1. Branch 57: char. 63: 2→3. Branch 58: char. 59: 1→3; char. 68: 1→2; char. 79: 1→2. Branch 59: none. Branch 60: char. 44: 2→0; char. 56: 3→4; char. 62: 1→0. Branch 61: char. 5: 3→4. Branch 62: char. 30: 0→1; char. 31: 0→1. Branch 63: char. 21: 3→1; char. 56: 3→4; char. 79: 1→2. Branch 64: char. 55: 1→2; char. 74: 0→1. Branch 65: char. 21: 6→7; char. 38: 0→2; char. 43: 0→2. Branch 66: char. 19: 2→0; char. 45: 0→6; char. 52: 1→0; char. 68: 2→3. Branch 67: char. 12: 0→1; char. 19: 2→4; char. 20: 0→B; char. 42: 2→0; char. 43: 0→6; char. 67: 2→1. Branch 68: char. 24: 1→0. Branch 69: char. 34: 3→0. Branch 70: char. 19: 2→0; char. 45: 0→4; char. 49: 0→1; char. 56: 3→2; char. 58: 1→0; char. 76: 0→2. Branch 71: char. 8: 0→1; char. 9: 0→1; char. 14: 0→1; char. 16: 0/3→2; char. 20: 0→8; char. 22: 2→1; char. 30: 0→4; char. 43: 0→7; char. 63: 0→7; char. 64: 0→1; char. 75: 0→1; char. 84: 2→3. Branch 72: char. 23: 0→1; char. 63: 0→4; char. 66: 0→1; char. 71: 0→2; char. 78: 2→A; char. 82: 0→1. Branch 73: char. 3: 0→1; char. 6: 3→2; char. 12: 0→2; char. 19: 2/B→C; char. 26: 1/5→0; char. 30: 0→6; char. 31: 0→6; char. 32: 3→2; char. 34: 0→3; char. 37: 0→2; char. 38: 0→2; char. 42: 2→0; char. 58: 1→0; char. 63: 0→8; char. 71: 0→3; char. 82: 0→1; char. 86: 2→1; char. 88: 4→3. Branch 74: char. 4: 1→0; char. 8: 0→1; char. 27: 2→1; char. 39: 2→8; char. 71: 0→5; char. 72: 0→2. Branch 75: char. 3: 0→1; char. 11: 0→1; char. 19: 2→C; char. 55: 1→2; char. 74: 0→7; char. 80: 1→0; char. 83: 0→3; char. 85: 0→4; char. 86: 2→1; char. 87: 1→0. Branch 76: char. 8: 0→2; char. 10: 0→1; char. 17: 1→3; char. 21: 8→0; char. 39: 2→0; char. 45: 0→5; char. 57: 1→2. Branch 77: char. 9: 2→1; char. 19: 2→4; char. 20: 0→8; char. 21: 8→4; char. 30: 0→4; char. 31: 0→4; char. 39: 2→6; char. 45: 0→4; char. 52: 1→0; char. 53: 1→0; char. 74: 0→5. Branch 78: char. 1: 0→1; char. 3: 0→1; char. 16: 0→1; char. 28: 0→2; char. 32: 3→2; char. 43: 0→4; char. 56: 1/2→4; char. 67: 1→2; char. 68: 4→2; char. 72: 0→1; char. 78: 2→8. Branch 79: char. 2: 0→1; char. 5: 2→0; char. 8: 2→0; char. 10: 0→1; char. 19: 2→3; char. 32: 3→5; char. 48: 0→2; char. 55: 1/2→0; char. 56: 1/2→5; char. 77: 1→0; char. 85: 0→4. Branch 80: char. 5: 2→1; char. 19: 2→A; char. 20: 0→8; char. 31: 0→4; char. 57: 1→4; char. 72: 0→1; char. 78: 2→7; char. 87: 0→1. Branch 81: char. 3: 0→1; char. 6: 3→2; char. 11: 0→2; char. 12: 0→2; char. 14: 0→1; char. 15: 0→1; char. 16: 0→3; char. 23: 1→0; char. 27: 2→1; char. 32: 3→5; char. 59: 0→9; char. 68: 4→2; char. 78: 2→C. Branch 82: char. 2: 0→1; char. 5: 2→0; char. 29: 0→3; char. 30: 0→7; char. 31: 0→7; char. 32: 3→2; char. 38: 0→2; char. 42: 2→0; char. 44: 2→0; char. 52: 1→0; char. 53: 1→0; char. 56: 1→3; char. 72: 0→1;

char. 78: 2→B. Branch 83: char. 23: 1→0; char. 37: 0→1; char. 45: 7→5; char. 73: 1→0; char. 77: 1→0. Branch 84: none. Branch 85: none. Branch 86: none. Branch 87: char. 6: 0→3; char. 35: 0→1; char. 40: 0→1; char. 58: 0→1. Branch 88: char. 39: 8→1; char. 86: 1→2. Branch 89: char. 4: 0→1; char. 73: 1→2. Branch 90: char. 7: 0→2; char. 9: 0→2. Branch 91: char. 14: 0→1; char. 39: 1→2. Branch 92: char. 21: 1→8; char. 71: 2→0; char. 87: 0→1. Branch 93: char. 18: 3→6. Branch 94: char. 14: 1→0; char. 53: 1→0; char. 54: 0→1. Branch 95: char. 1: 0→2; char. 9: 2→0; char. 28: 0→4. Branch 96: char. 7: 2→0; char. 52: 1→0; char. 74: 0→4; char. 78: 2→3. Branch 97: char. 43: 0→7; char. 54: 1→0. Branch 98: char. 23: 0→1; char. 44: 2→0; char. 68: 3→4; char. 74: 4→2. Branch 99: char. 5: 2→4; char. 16: 0→1; char. 36: 0→1; char. 87: 1→0. Branch 100: char. 80: 1→0. Branch 101: none. Branch 102: char. 32: 3→2; char. 57: 1→3. Branch 103: none. Branch 104: char. 19: B→C; char. 20: 0→9; char. 22: 2→0; char. 23: 1→0; char. 74: 2→7; char. 88: 4→3. Branch 105: char. 44: 0→2; char. 46: 0→1; char. 59: 4→8; char. 77: 1→0; char. 78: 3→1; char. 83: 0→2; char. 86: 2→0. Branch 106: char. 52: 0→1; char. 53: 0→1; char. 88: 3→1. Branch 107: char. 24: 1→0; char. 37: 0→1. Branch 108: char. 55: 3→2; char. 69: 5→4. Branch 109: char. 21: 0→1; char. 32: 3→2. Branch 110: char. 63: 0→6; char. 69: 5→4. Branch 111: char. 50: 0→1. Branch 112: char. 3: 1→2; char. 59: 4→3. Branch 113: char. 44: 0→2; char. 74: 2→0; char. 77: 0→1. Branch 114: char. 1: 2→1; char. 32: 3→0; char. 39: 2→0; char. 56: 2→4; char. 69: 5→3; char. 70: 5→3; char. 71: 0→2; char. 78: 3→6; char. 80: 1→2. Branch 115: char. 57: 1→3. Branch 116: char. 39: 0→7; char. 55: 1→2. Branch 117: char. 88: 4→2. Branch 118: char. 60: 2→0; char. 61: 0→1; char. 69: 3→1. Branch 119: char. 55: 2→3; char. 70: 3→0. Branch 120: char. 60: 0→1; char. 88: 2→1. Branch 121: char. 22: 2→3; char. 70: 0→1. Branch 122: char. 31: 0→2. Branch 123: char. 38: 0→2; char. 42: 2→0. Branch 124: char. 22: 2→3. Branch 125: char. 39: 7→5; char. 50: 0→1; char. 70: 3→4; char. 85: 0→3. Branch 126: char. 38: 0→2. Branch 127: char. 29: 0→2; char. 31: 0→2. Branch 128: char. 18: 0→2; char. 19: 0→4; char. 21: 0→2; char. 30: 0→2; char. 42: 2→0. Branch 129: char. 59: 5→0. Branch 130: char. 60: 2→1. Branch 131: char. 19: 4→7; char. 20: 2→6; char. 61: 0→1. Branch 132: char. 60: 1→0; char. 69; 3→0; char. 70: 3→0. Branch 133: char. 20: 0→1; char. 63: 0→1: char. 84: 0→1. Branch 134: char. 16: 0→1: char. 42: 2→0. Branch 135: char. 5: 2→4; char. 18: 0→2; char. 19: 0→7; char. 21: 0→2; char. 23: 0→1. Branch 136: char. 30: 0→3; char. 56: 2→1; char. 63: 1→0; char. 68: 3→4. Branch 137: char. 16: 1→0; char. 74: 4→5. Branch 138: char. 58: 1→0. Branch 139: char. 5: 2→4: char. 58: 1→0. Branch 140: char. 39: 2→0; char. 55: 1→0; char. 56: 2→3; char. 67: 1→2; char. 68: 3→2; char. 84: 0→2. Branch 141: char. 7: 2→1; char. 32: 3→2; char. 59: 0→1. Branch 142: char. 34: 0→3. Branch 143: char. 3: 0→1; char. 7: 1→0; char. 39: 0→1. Branch 144: char. 6: 3→0; char. 11: 0→2; char. 12: 0→2; char. 27: 2→0. Branch 145: char. 5: 2→3; char. 21: 6→3; char. 33: 0→2; char. 39: 1→2; char. 45: 0→3; char. 54: 1→0; char. 75: 0→1; char. 79: 0→1. Branch 146: char. 62: 0→1; char. 68: 2→1. Branch 147: none. Branch 148: char. 20: 0→4. Branch 149: char. 43: 0→1. Branch 150: char. 30: 0→3; char. 33: 2→0; char. 63: 5→2. Branch 151: char. 23: 0→1; char. 29: 0→2; char. 31: 0→3; char. 34: 3→0; char. 38: 0→2; char. 42: 2→0; char. 43: 1→7; char. 62: 1→0. Branch 152: char. 45: 3→1; char. 52: 1→0; char. 59: 1→0; char. 67: 3→2; char. 75: 1→0; char. 78: 0→1/2; char. 79: 1→0. Branch 153: char. 5: 3→4; char. 43: 7→5; char. 56: 3→2. Branch 154: char. 63: 2→1; char. 76: 0→1. Branch 155: char. 34: 0→2; char. 44: 2→0; char. 68: 1→2. Branch 156: char. 34: 0→1. Branch 157: char. 63: 2→1. Branch 158: char. 37: 0→1; char. 76: 0→1. Branch 159: char. 43: 7→5; char. 79: 0→3; char. 80: 1→3. Branch 160: char. 11: 2→3; char. 44: 2→0; char. 47: 0→1. Branch 161: char. 68: 1→2. Branch 162: char. 48: 0→1. Branch 163: char. 13: 0→1; char. 37: 0→1; char. 58: 1→0; char. 71: 0→3. Branch 164: char. 56: 3→6; char. 68: 2→0; char. 71: 0→2; char. 82: 0→1. Branch 165: char. 6: 3→2; char. 11: 0→1; char. 21: 6→5; char. 32: 2→3. Branch 166: char. 35: 1→0; char. 59: 0→9; char. 77: 1→0. Branch 167: char. 12: 0→1; char. 18: 3→0; char. 28: 0→1; char. 63: 0→7; char. 71: 0→1.

APPENDIX 4

For detailed information on specimens studied, the reader should refer to the 'material examined' sections in Gassmann (1999), Gassmann (2000) and Gassmann & Hämäläinen (2002). Additional taxa/specimens examined for the present study are listed in the following.

Collections:

BMNH = Natural History Museum: British Museum (Natural History), London.

HLMD = Hessisches Landesmuseum, Darmstadt.

ISNB = Institut Royal des Sciences Naturelles, Brussels.

RMNH = National Museum of Natural History (Naturalis; formerly: Rijksmuseum van Natuurlijke Historie), Leiden (including the former Roland Müller collection).

SMFD = Senckenberg-Museum, Frankfurt.

Allocnemis leucosticta: **South Africa, Cape Province**: 4♂, Natal, Durban, 8.iii.1939, RMNH. 2♂, Klein-Swartberge, Seweweekspoort Pass, 5.i.1951, Swedish S. Africa Exped. 1950-1951, RMNH.

Arabicnemis caerulea: **Arabian Peninsula, Oman**: 1♂, Wadi Al-Abyadh, appr. 21°32'N 56°18'E, 16.ix.1988, ex Oman Nat. Hist. Mus., HLMD-Od 226, HLMD.

Arrhenocnemis amphidactylis: **New Guinea, West Papua**: 1♂ (paratype), central New Guinea, above Bernhard Camp, 700 m, 29.iii.1939, RMNH.

Asthenocnemis stephanodera: **Philippines, Palawan Island**: 1♂, Quezon, Lamakan, Magmuni str, 27.v.-1.vi.1991, RMNH. 1♂, Quezon, Lamakan, Magmuni str, 1000 ft., 16-22.v.1991, RMNH. 1♀, Quezon, Magmuni str, 1000 ft., 16-22.v.1992, RMNH.

Calicnemia eximia: **China, Hainan**: 1♂, China, Central Hainan Island, Tongshi City, Tongshi Holiday Resort, 400 m, 28.vi.1993, RMNH. **India, Assam**: 1♂, Assam, Shillong, 25.vi.1974, RMNH. **India, West Bengal**: 1♀, Bom Busty, 1.vi.1976, RMNH. 1♂, 1♀, Gumpha, 6.vi.1976, RMNH. 1♂, Kapkot, 26.ix.73, RMNH. 1♂, Loharkhet, 26.ix.73, RMNH. **India, Sikkim**: 1♀, Koolloo [Kooloo?], Carleton, ISNB. 1♂, ex Staudinger, acq. 1903, RMNH. 1♂, ex Mus. Ann Arbor (coll. Forster), acq. 1936, RMNH. **Nepal**: 1♂, Barabhise, Tibettan frontier, ca. 950 m, 4.vi.1973, RMNH. 2♂, Charnavati Khola/pine for., 1200 m, 15.ix.74, RMNH. 1♂, Kathmandu valley, Waterfall west Chaunica, 1400 m, 24.v.1973, RMNH. 14 (juv.), 1♀, Kodari, Tibettan frontier, ca. 1700 m, 4.vi.73, RMNH. 1♂, Rhedi, 1520 m, 14.ix.74, RMNH.

Coeliccia membranipes: **Indonesia, Java**: 1♂, W. Java, Salak, 800 m, 31.x.60 [1961?, different labels], ex coll. A. Heymer, RMNH. **Indonesia, Nias Island**: 1♂, Central Nias Island, Lahago, 4.ii.-10.iii.1896, RMNH. **Indonesia, Sumatra**: 1♂, Bambar Baru, 950 m, 12.xi.50, RMNH. 1♂, Fanangtalu, Ophir Distrikten, Pad. Bovenland, v.1915 [1914 ?]. 1♂, Fort de Kok, x.1913. 1♀, Moesa Kambangan, 10.ix.1927. 2♂, N. Sumatra, Atjeh, Sangir, 1200 m, 19.iii.1937. 1♂, N.E. Sumatra, Sibolangiti, 400 m, 17.xi.1950. 2♂, S. Sumatra, S.W. Lampoeng, Mt Tanggamoes, 3.i.35. 2♂, S. Sumatra, S.W. Lampoeng, Mt Tanggamoes, 24.xii.34, RMNH. 2♂, S. Sumatra, Wai Teboe, 500 m, 24.vi.1934. 1♂, Sumatra Sungai Kumbang (Kurintji), ix.1915, RMNH. 1♀, Sumatra, Serapai (Kurintji), vii.1915. 1♂, Sumatra, Bengkulen, Suban Ajam (Redjang), vii.1916. 1♂, Suban Ajam (Redjang) Bengkulen, vii.1916. 2♂, Weg B. Agoeng, grens Benkoelen, Ranaumeer, 2.i.1938, RMNH.

Copera marginipes: **Indonesia, eastern Java region**: 1♂, Kangean Island, 21.ix.54, Petafan, RMNH. **Indonesia, Bali**: 1♂, 1♀, ca. 2 km inland from Grokgak, 8°11'S 114°47'E", 150 m asl., 11.v.1991, RMNH.

Cyanocnemis aureofrons: **New Guinea, West Papua**: 5♂, 2♀, paratypes, Araucariakamp, 700-800 m, 8.-31.iii.1939, RMNH. All paratypes; Neth. Ind.-Amer. New Guinea Exped., RMNH.

Idiocnemis leonorae: **Papua New Guinea**: 3♂, 2♀, NE New Guinea, E. Highlands, Yonkie Dome, 11 mi. NE Kainantu, 1500 m, 18-20.x.1972, ex coll. Donnelly, RMNH.

Indocnemis orang: **SE Asia, Malayan Peninsula**: 2♂, Malaya, Selangor, Templer Park, K. L., 12-13 mi., 21.iii.1963, RMNH. 1♂, Malaya, S. Kedah, Bading, Badenoch Estate, 21.ii.1963, RMNH.

Leptocnemis cyanops: **Seychelles, Mahé island**: 1♂, banks of the Grand Bois R., 6.ii.1974, RMNH. 1♂, Bouin, 15.ii.1974 RMNH. 1♂, St. Louis R., 8.ii.1974, RMNH. **Seychelles, Praslin island**: 1♂, Vallée de Mai, 25.vii.1965, ex coll. Pinhey '66, RMNH.

Lieftinckia isabellae: 2♂ (1 def.), **Solomon Islands, Santa Ysabel island**, Maring distr., Ta Matahi, 2.vii.1960, ex BISH, RMNH.

Lieftinckia kimminsi: Paratypes: 1♂, **Solomon Islands, southern Bougainville**, west Kieta, Crown Prince Range, Kokorei (=Kokuze), 900 m, 12.vi.56, RMNH. 1♂, 1♀, west Kieta, Crown Prince Range, Kokorei (=Kokuze), 9.vi.56, RMNH.

Lieftinckia malaitae: Paratypes: 2♂ (1 juv., incompl.), 1♀ (semi-adult), **Solomon Islands, Malaita Island**, Dala, 50 m, 9-4.vi.1969, RMNH. 2♂ (1 semi-adult), Ngwaian, 1500 ft., 10.x.1967, RMNH.

Lieftinckia ramosa: Paratype: 1♂, **Solomon Islands, Bougainville island**, RMNH.

Lieftinckia salomonis: 2♂, 1♀, **Solomon Islands, Guadalcanal island**, Gold Ridge, 30.vi.1956, BMNH (no. BM 1956-712). 1♀, Sornolio R. [?], 30.vi.1956, BMNH (no. BM 1956-712). 1♀, Tenaligi R., 25.ix.65, "Dicht bos; juv., white", RMNH.

Lochmaeocnemis malacodora: 2♂, **New Guinea, West Papua**, Araucaria Camp, 800 m, iii.1939. 24, Lower Mist Camp, 1400-1600 m, i.1939. 6♂, 2♀, Rattan Camp, 1200 m, ii-iii.1939. All paratypes; Neth. Ind.-Amer. New Guinea Exped., RMNH.

Mesocnemis singularis: **East Africa**: 3♂, Rusinga Island, Lake Victoria, iii.1950, RMNH. 3♀, Jinja, Uganda, vi. 1949, RMNH. 1♀, Victoria Falls, 29.ix.1961, RMNH. 2♂, Ghana (Eastern Region), 31 km NW Koforidua: Birim R. at Bunso Waterworks. 6°16.0'N 0°28.3'W, 10.v.2000, RMNH.

Paracnemis alluaudi: **Madagascar**: 1♂, Fort-Dauphin, 17.ii.58, RMNH. 1♀, Soanierana-Ivongo, 10.xi.57, RMNH.

Paramecocnemis erythrostigma: **New Guinea, West Papua**: 4♂ paratypes, Hollandia, iv.-vi.1931 RMNH. 3♂, Hollandia, vii.1938, Dutch-Amer. New Guinea Exped. 1938-1939, RMNH.

Platycnemis pennipes: **Europe, France**: 1♂, Dampierre, bij Parijs, 19.vi.1966, RMNH. **Europe, Turkey**: 1♂, 1♀, Mugla, ca. 7 km SW of Köycegiz: Lamnan Çayi, near bridge SW of Hamitköy, 5 m asl, 1.vi.2000, RMNH.

Rhyacocnemis sufficiens: **Papua New Guinea, D'Entrecasteaux Islands**: 1♂ paratype, Goodenough I., 1600 m – Camp (4th Archbold New Guinea Exped.), 12.x.1953, RMNH. 1♂, Normanby I., Camp 2 (5th Archbold New Guinea Exped.), Mt Pabinama, 820 m, 8.v.1956, RMNH. Archbold Exped.

Risiocnemis appendiculata: **Philippines, Mindanao Island, Misamis Oriental Province**: 3♂, 1♀, Bal-ason, 2-3.iv.1960, RMNH. **Philippines, Mindanao Island, South Cotabato Province**: 2♂, Koronadal, Barrio 8, 4.ii.1994, RMNH. 1♂, Mt Matutum, 500-700 m, 16-19.ix.1993, RMNH. **Philippines, Mindanao Island, Surigao del Sur Province**: 1♂ (def.), Cotabato, Parang, 13.i.1954, RMNH. 3♂, Tandag, Hitaub Creek, 500-600 m, 16-19.iv.1995, RMNH. **Philippines, Leyte Island**: 1♂, Ormoc, 18.xi.1966, RMNH.

Risiocnemis arator: **Philippines, Luzon Island, Ifugao Province**: 1♂, Jacmal Bunhian, 24 km E Mayoyao, 800-1000 m, 7-8.iv.1967, RMNH. **Philippines, Luzon Island, Nueva Viscaya Province**: 1♂, 1♀, Sta Fe, Dalton Pass, 800-1200 m, 25-30.vi.1989, RMNH.

Risiocnemis asahinai: **Philippines, Mindoro Island**: 1♂, Barrio Luyang, Halcon Mts., 360-500 m, 14./17.v.1991, RMNH. 3♂, Mindoro Oriental Province. Calapan, Comonal, Mt Tarugin, ca. 350 m, 21./29.vi. & 17./26.vii.1990, RMNH. 2♂, 4♀, Mt Halcon, 1000-1500 m, 2-20.v.1994, RMNH.

Risiocnemis confusa: **Philippines, Catanduanes Island**: 1♂, Gigmoto, San Pedro, Tongao Creeks, 400-500 m, 20-30.vi.1996, RMNH.

Risiocnemis elegans: **Philippines, Luzon, Aurora Province**: 7♂, 1♀, Dinalungan, Mt Anaguao, Alebit R. area, 600-900 m, 9-14.iii.1997, RMNH. 2♂, Dinalungan, Mt Anaguao, Bolawan R., 800-1000 m, 11.iii.1997, RMNH.

Risiocnemis erythrura: **Philippines, Mindanao Island, Surigao Province**: 1♂, L. Mainit, 30.xi.1989, RMNH. **Philippines, Mindanao Island, Surigao del Sur Province**: 1♂, 1♀, Carmen, Upper Tandag R., km 9 Lanang Line, 500 m, 24.iv.1995, RMNH. 1♂, Tago, Meme R., 100-300 m, 12-18.vi.1996, RMNH.

Risiocnemis gracilis: **Philippines, Luzon Island, Nueva Ecija Province**: 1♂, 1♀, Caranglan, Batching R., 700-850 m, 11.vi.1991, RMNH. **Philippines, Luzon Island, Nueva Viscaya Province**: 1♂, 1♀, Sta Fe, Dalton Pass area, 900 m, 8-17. viii.1991, RMNH.

Risiocnemis kiautai: **Philippines, Sibuyan Island**: 1♂, paratype, Magdiwang, Katingas, 29.iii.1987, RMNH. 1♂, paratype, Magdiwang, Tampayan, Camp Ga-ong, 80-150 m, 1-12.iv.1987, RMNH.

Risiocnemis laguna: **Philippines, Luzon Island**, Laguna Province: 1♂, 1♀, paratypes, Paete, 29.vi.1916, SMFD.

Risiocnemis moroensis: **Philippines, Mindanao Island, Bukidnon Province**: 1♂, Philippines, Mindanao, Bukidnon, Mt Imbayo, 30.viii.1988, RMNH. 1♂, 2♀, Mt Kalatungan, Talakag, Brgy Mebadiang, Magamanason Creek, Sitio Olayan, 1000-1100 m, 5-18.viii.1995, RMNH. 1♀, Philippines, Mindanao Id, Bukidnon, Mabadiang, Olayan, Mt Kalatungan, Muntian Creek, 1200-1400 m, 24./25.xi.1995, RMNH. 2♀, Philippines, Mindanao Id, Bukidnon, Mebadiang, Dumatap, Mt Kalatungan, Mansabilan Creek, 1000-1300 m, 24.xi.1995, RMNH. 1♂, Mt Katanglad, Impasugong, Brgy Impalutao, Gantongan Creek, 800-900 m, 19-29.viii.1995, RMNH.

Risiocnemis praeusta: **Philippines, Dinagat Island**: 1♂, Loreto, Balitbiton, Mt Canbinlio, vii.1989, RMNH. **Philippines, Leyte Island**: 1♀, (Mt Balocaue ?), 20.i.1989, RMNH. **Philippines, Panaon Island**: 1♂, San Francisco, Gabing Gamay, big river, x.1988, RMNH. 1♂, 1♀, San Francisco, Batong Lapad, viii.1988, RMNH.

Risiocnemis pulchra: **Philippines, Luzon Island, Bataan Province**:1♂, paratype, Luzon, Limay, 21.x.1913, SMFD. **Philippines, Luzon Island, Zambales Province**: 6♂, 2♀, Masinloc, Mt Coto, Tal-tal, 400-700 m, 1-8.iv.1997, RMNH.

Risiocnemis rolandmuelleri: **Philippines, Negros Island**: 9♂, 1♀, Silay, Patag, Cuyong R., Dumalabdab Falls, 700-750 m, 22.v.1996, RMNH.

Risiocnemis seidenschwarzi: **Philippines, Cebu Island**: 4♂, paratypes, Tabunan, 500 m, 19.xi.1998 & 9.ii.1999, RMNH.

Risiocnemis serrata: **Philippines, Catanduanes Island**: 3♂, 1♀, Gigmoto, San Pedro, Simohe Creeks, 300-500 m, 20-30.vi.1996, RMNH. **Philippines, Luzon, Bataan Province**: 2♂ (1 def.), Los Baños, 15.v.1977, RMNH. 22, Los Baños, 50 m, 28.v.1949, RMNH.

Risiocnemis varians: **Philippines, Luzon Island, Nueva Viscaya Province**: 1♂, Dalton Pass, Sta Fe, Atbo, 500-900 m, 13.ii.1989, RMNH. 1♂, Dalton Pass, Sta Fe, Torner, 500-900 m, 12.ii.1989, paratype, RMNH. 2♀, Dalton Pass, Sta Fe, Zigsag, 500-900 m, 16.ii.1989, paratype, RMNH. 3♂, 3♀, Sta Fe, Barrio Lohong, Mounts east of Dalton Pass, 900-1000 m, 10-23.i.1993, RMNH. 2♂, Sta Fe, Dalton Pass, 800-1200 m, 25./30.vi.1989 & 5./18.vi.1990, Paratype, RMNH. 1♀, Sta Fe, Atbo R., 550-800 m, 10.vi.1991, RMNH. 1♂, Sta Fe, Dalton Pass area, 900 m, 8./17.viii.1991, RMNH. **Philippines, Luzon Island, Quirino Province**: 1♂, 1♀, Maddela, Sulong R., 500-650 m, 26./27.iv.1991, RMNH.

Salomocnemis gerdae: **Solomon Islands, Guadalcanal**: 1♂, Komugelea, forest, 1200 ft., 22.ix.1965, RMNH. 1♀, Komugelea, Guadalcanal, open brook, 1200 ft., 22.ix.1965, RMNH.

Stenocnemis pachystigma: **Western Africa, SW Cameroon**: 1♂, Meme, Nyasoso, Mt Kupe, R. Nyesosoh, water catchment, 920 m, 30.iii.1997, RMNH. 1♀, Tombel, Nyasoso, Mt Kupe, Shrike Trail, 920 m, 5.iv.1995, RMNH.

Thaumatagrion funereum: **Northern New Guinea**: 6♂, paratypes, Hollandia, iii.1931, RMNH. 1♂, 1♀, Hollandia, 24.i.1933, RMNH.

Torrenticnemis filicornis: **Central northern New Guinea**: 5♂, paratypes, Lower Mist Camp, 1400-1600 m, i.1939, RMNH. 5♂, 1♀, paratypes, Sigi Camp, 1500 m, ii.1939. Neth. Ind. - Amer. New Guinea Exped., RMNH.

Bonner zoologische Beiträge | Band 53 (2004) | Heft 1/2 | Seiten 81–97 | Bonn, Juni 2005

Neue *Zygaena*-Taxa aus Südosteuropa, Vorder- und Zentralasien (Lepidoptera: Zygaenidae)[1]

Für Clas, dem wir alle viel verdanken

Axel HOFMANN, Breisach-Hochstetten

Abstract. Several new taxa of the genus *Zygaena* Fabricius, 1775 are described from south-eastern Europe, Anatolia, Iran, Pakistan and Central Asia: *Zygaena (Mesembrynus) rubricollis arachosica* subsp. nov. from Quetta region (Pakistan) with *Z. manlia*-like forewing spots. *Zygaena (Mesembrynus) rubricollis shahkuhica* subsp. nov. from Shah-Kuh (Iran) where it occurs syntopically with *Z. manlia* and *Z. cacuminum*. *Zygaena (Mesembrynus) nocturna eberti* subsp. nov. from the central Zagros range (Iran) typical with connected spots 5+6. *Zygaena (Agrumenia) magiana pamirescens* subsp. nov. from Kirghistan, a subspecies with yellow forewing spots thus reminiscent of *Z. pamira*. *Zygaena (Agrumenia) formosa molleti* subsp. nov. from Bolkar Dagh (Turkey), the first high mountain population of this species, ecologically and phenotypically reminiscent of *Z. peschmerga*. *Zygaena (Agrumenia) tenhagenova* sp. nov. from Iranian Kordestan, a distinct biospecies closely related to *Z. chirazica* and *Z. naumanni*. *Zygaena (Agrumenia) haberhaueri demangei* subsp. nov. from north-western Iran, with red abdominal cingulum on 1 – 3 segments. *Zygaena (Zygaena) viciae pelopis* subsp. nov. from Peloponnesos peninsula (Greece) reminiscent of *Z. filipendulae* and *Z. vicae laphria* from the Taurus range in Turkey. *Zygaena (Zygaena) filipendulae wiegelorum* subsp. nov. from the province of Kars (Turkey) with red confluent forewing spots. *Zygaena (Zygaena) lonicerae pseudangelicae* subsp. nov. from Lake Van region (Turkey) phenotypically similar to *Z. angelicae* and *Z. trifolii*.

Key words: *Zygaena chirazica, Z. filipendulae wiegelorum* subsp. nov., *Z. formosa molleti* subsp. nov., *Z. haberhaueri demangei* subsp. nov., *Z. lonicerae pseudangelicae* subsp. nov., *Z. magiana pamirescens* subsp. nov., *Z. naumanni, Z. nocturna eberti* subsp. nov., *Z. rubricollis arachosica* subsp. nov., *Z. r. shahkuhica* subsp. nov., *Z. tenhagenova* sp. nov., *Z. viciae pelopis* subsp. Nov.

1. EINLEITUNG

Bei der Abfassung des „Systematic Catalogue of the Zygaeninae“ (HOFMANN & TREMEWAN 1996) zeigte sich bereits, dass einige sehr auffällige Populationsgruppen auch aus relativ gut bearbeiteten Regionen wie der Türkei und Griechenland bislang noch unbenannt geblieben sind. Die Beschreibung dieser Taxa wird hiermit nachgeholt. Des weiteren werden hier einige besonders markante Neuentdeckungen der vergangenen Jahre aus Zentralasien, dem Iran und aus Pakistan namentlich verfügbar gemacht.

Eigene Aufsammlungen der Jahre 2001 bis 2004 im Iran (zusammen mit A. KALLIES, J. U. MEINEKE , W. G. TREMEWAN) sowie Beobachtungen von T. KEIL und G. TARMANN haben den Verdacht erhärtet, dass unter *Zygaena* (*Mesembrynus) rubricollis* Hampson, 1900 bislang mehr als eine einzige Biospezies zusammengefasst wurde (HOFMANN & TREMEWAN 2003; KEIL 2003). Gleiches scheint für *Zygaena* (*Mesembrynus*) *seitzi* Reiss, 1938, *Zygaena* (*Mesembrynus*) *manlia* Lederer, 1870 und *Zygaena* (*Agrumenia*) *rosinae* Korb, 1903 zuzutreffen. HOFMANN & TREMEWAN (2003) haben neuerdings einen ersten vagen Versuch unternommen, die komplizierten taxonomischen Verhältnisse zu entwirren. Als Ergebnis wurden *Z. aisha*, *Z. nocturna* und *Z. fredi* wieder in den Artstatus erhoben. Unklar bleiben aber nach wie vor zahlreiche Zuordnungen (*kermanensis, qashqai, askarii, taftanica, escaleraiana, tenhageni* etc.), und es bedarf noch intensiver Feldarbeit sowie umfassender biologischer und taxonomischer Untersuchungen, bis die Verwandtschaftsverhältnisse insbesondere der irano-afghanischen *Mesembrynus*-Arten einigermaßen befriedigend erklärt werden können. Auf die noch ungenügend begründete Taxonomie bei *Z. afghana, Z. rosinae*/*sengana* hat KEIL (2003) hingewiesen und *Z. sengana* wieder als bona species abgetrennt. Ein Artenkomplex könnte sich auch hinter *Z. chirazica*/*naumanni* verbergen. Es ist bekanntermaßen bei allopatrischen Taxa oft schwer zu entscheiden, ob es sich um eine einzige außergewöhnlich differenzierte, polytypische Art oder um mehrere engverwandte isolierte Biospezies handelt. Die geographische Isoliertheit und der bisweilen hohe Grad an Verschiedenheit z. B. zwischen *Z. naumanni*, *Z. chirazica chirazica* und *Z. chirazica eckweileri*, aber auch die Unterschiede zu anderen bislang noch nicht beschriebenen Populationen bzw.Taxa (s. *Z. tenhagenova* n. sp. , Populationen vom Zarde-Kuh und von Delijan) könnten bereits als Argumente für distinkte Biospecies angeführt werden. Es muss jedoch betont werden, dass diese „Artverschiedenheit“ bisher eher schwach begründet wurde. Dies gilt für *Z. naumanni* aus der Region um Chonsar und Fereydun Shahr, aber auch für die hier neu beschriebene *Z. tenhagenova* n. sp. aus iranisch Kurdistan. Eine Beschreibung als Unterart von *Z. chirazica* wäre nur möglich gewesen, wenn man *Z. naumanni*, die geographisch dazwischen siedelt, zuvor eingezogen hätte. Die nördlichste Population unweit Delijan zeigt bereits habituelle Annäherung an *Z. haberhaueri*, so dass evtl. auch diese Art in die Untersuchung mit einbezogen werden müsste. Geeignete Feldstudien (z. B. Anlockversuche mit virginen Weibchen, Aufsammlungen in bislang unbesammelten Kontaktbereichen), Zucht- und Kreuzungsexperimente und die gezielte Suche nach weiteren taxonomischen Merkmalen (z. B. GU-Serienuntersuchungen) werden zukünftige Aufgabenbereiche darstellen, verbunden mit der Hoffnung, weitere brauchbare Hinweisen zu erhalten, ob unsere heutigen Anschauungen richtig waren oder korrigiert werden müssen.

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[1] Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004) zum Gedenken

Wichtige Argumente zur Rekonstruktion stammesgeschichtlicher Verwandtschaftsverhältnisse wird uns die Analyse geeigneter DNA-Abschnitte liefern (O. NIEHUIS, Bonn, in Vorbereitung). Entscheidungen auf Artniveau (und tiefer), insbesondere die Bewertung allopatrischer Taxa (Allo- oder Konspezifität), wird dem Taxonomen aber auch von diesem Wissenschaftszweig mit Sicherheit nicht abgenommen werden können. Es wäre vermessen zu erwarten, dass genetische Schwellenwerte gefunden würden oder definierbar wären, die eine solche Entscheidung fortan dem wertneutralen Computer überließen.

2. BESCHREIBUNG NEUER TAXA

Die nachfolgenden Unterarten werden hier vorerst den derzeit noch gültigen Taxa zugeordnet.

Zygaena (Mesembrynus) rubricollis arachosica subsp. nov.

(Figs. 1 – 3)

Zygaena (*Mesembrynus*) *rubricollis* Hampson, 1900, Journal of the Bombay natural History Society 13: 224, pl. B, fig. 9

Derivatio nominis: Nach der altpersischen Satrapie „Arachosien“.

Holotypus, ♂: „Pakistan, Baluchistan, Quetta/Urak, 2400 – 2700 m, 24. – 26.V.83, leg. ECKWEILER“, coll. A. HOFMANN (später deponiert in coll. Staatliches Museum für Naturkunde Karlsruhe, SMNK).

Paratypen: 1 ♂, 2 ♀♀, Daten wie Holotypus, coll. A. HOFMANN; 3 ♂♂, 3 ♀♀, Daten wie Holotypus, jedoch 23. – 24.V. 1979, coll. A. HOFMANN. Einzelne Belegtiere (Daten wie Holotypus) in coll. C. M. NAUMANN und coll. T. WITT (via coll. G. REISS).

Zum Vergleich liegen Topo- und Paratypen der aus Afghanistan beschriebenen Unterarten (*Z. r. afghanica* Reiss, 1940; *Z. r. flavicola* Naumann, 1969; *Z. r. kabulica* Naumann, 1974; *Z. r. nasukmiri* Naumann, 1974) sowie aktuelle Nachfänge der nominotypischen Unterart von *Z. rubricollis* aus Nord-Pakistan (Birmoghlash, Chitral: leg. W. ECKWEILER 1983, leg. J.-C. WEISS 1996, leg. M. NICOLLE 1997) vor. Neuerdings wurde die Art auch weiter östlich im Nanga Parbat-Gebiet gefunden (DESSE 2003). Alle diese Populationen unterscheiden sich von *Z. r. arachosica* subsp. nov. durch ihre unverkennbare Tendenz zur Reduktion von Fleck 6 (insbesondere im costalen Bereich) sowie ein wesentlich kleineres Fleckenpaar 3+4. Bei der Nominatunterart, bei *Z. r. afghanica* und *Z. r. nasukmiri* ist dieses nicht selten sogar durch eine schwarze Ader deutlich in zwei separate Flecken aufgelöst. *Z. r. arachosica* subsp. nov. besitzt stets einen vollentwickelten “Nierenfleck” (= Fleck 6), der sich mit seinem oberen und unteren Ende Fleck 5 annähert und dadurch eine geknickte Form erhält. Fleck 5 ist meist von dreieckiger Gestalt, ebenfalls groß wie auch die Basisflecken 1+2 und das Fleckenpaar 3+4, die jeweils zu einem einzigen Flecken zusammenfließen. Insgesamt sind alle Flecken größer als bei den zuvor genannten Taxa, so dass eine gewisse Ähnlichkeit mit *Z. manlia* Lederer, 1870, entsteht. Rote Halskrause und geschlossenes Abdominalcingulum sind auf einem Segment vorhanden. Hinterflügelumrandung schmal, am beginnenden Analfeld nur schwach verstärkt. Hinterflügel wie bei allen afghanischen und pakistanischen Populationen ohne hyalinen Wisch. Hierdurch unterscheiden sich die afghanisch-pakistanischen *Z. rubricollis*-Taxa auch habituell ziemlich deutlich von weiter westlich anschließenden und ebenfalls heute (noch?) unter *Z. rubricollis* subsumierten iranischen und armenisch-südostanatolischen Populationen.

Zygaena (Mesembrynus) rubricollis shahkuhica subsp. nov.

(Fig. 7)

Derivatio nominis: Nach der Typenlokalität am Shah-Kuh (Prov. Mazandaran/Golestan).

Holotypus, ♂: „Mazandaran, Shah Kuh (Est), versant nord, 2800 – 3000 m, 15./17. 7.1998, leg. B. MOLLET“, coll. A. HOFMANN (später deponiert in coll. SMNK).

Dieses interessante Einzeltier wurde von B. MOLLET zusammen mit einer kleinen Serie *Z. cacuminum* Christoph, 1877, erbeutet. Gezielte Nachsuche seither blieb erfolglos. In den darauffolgenden Jahren konnten jedoch im selben Gebiet, unweit Hadjiabad topotypische *Z. manlia manlia* erstmals seit mehr als 130 Jahren wieder in wenigen Exemplaren nachgefangen werden (B. MOLLET 2000; B. MOLLET & G. FLUTCH 2001; G. EBERT, R. TRUSCH, H. ALIPANAH, E. EBRAHIMI 2003). Somit kann nun eine Verwechslung mit einer dieser beiden nahe verwandten Arten ausgeschlossen. Ich zögere nicht, diese Population anhand eines einzigen Exemplars mit einem Namen zu belegen, zumal das hier neu beschriebene Taxon sicherlich nicht zu *Z. manlia* oder *Z. cacuminum* gehört und *Z. rubricollis* aus dem gesamten Elbursgebirge bislang unbenannt geblieben ist (NAUMANN et al. 1984: 76 – als *Z. araxis* –, HOFMANN 2000). Weiter westlich, aus dem zentralen Elburs, liegen zum Vergleich einige wenige Tiere von *Z. rubricollis* (s. HOFMANN 2000: 227, leg. J. KLIR) vor. Sie sind jedoch abweichend gezeichnet, weshalb sie nicht zur Typenserie gezogen werden können. Insbesondere die Vorderflügelflecken sind größer, die Nierenmakel ist geknickt und das Basisfleckenpaar 1+2 schließt fast senkrecht zum Innenrand hin ab. Durch Reduktion von Fleck 2a ist bei *Z. r. shahkuhica* subsp. nov. der Basisfleck am Innenrand deutlich eingebuchtet. Fleck 5 und 6 sind völlig freistehend, die Nierenmakel steht fast senkrecht und besitzt keine „birnenförmige" Verdickung am unteren Ende. Der sichtbare Bereich der schwarz beschuppten Valven ist mit roten Schuppen durchsetzt. In Linneana Belgica XVIII: 229 (fig. 17) wurde das Tier bereits abgebildet. Die Unterschiede zu *Z. manlia* als auch zu *Z. cacuminum* und allen bekannten *Z. rubricollis*-Unterarten sind signifikant. Position und Größe der Flecken 5 und 6 erinnern am ehesten an die von NAUMANN & NAUMANN (1980) als Unterart von *Z. manlia* beschriebene, inzwischen zur Art aufgewertete *Z. aisha* (HOFMANN & TREMEWAN 2003) aus Kerman. Hierbei scheint es sich jedoch um eine ökologisch und morphologisch wohl differenzierte endemische Biospezies aus den isolierten Gebirgen der Provinz Kerman zu handeln.

Als gesichert kann nun angesehen werden, daß mindestens drei verschiedene Arten aus der *manlia-cuvieri*-Gruppe im Elbursgebirge vorkommen. Erschwert wird die Bewertung der einzelnen Vorkommen durch überraschend spärliche Nachweise. Während im Zagrosgebirge *Z. manlia* oder *Z. fredi* an manchen Standorten in Anzahl beobachtet werden können, sind aus dem Elburs immer nur Einzeltiere bekannt geworden.

Zygaena (Mesembrynus) nocturna eberti subsp. nov.

(Figs. 13 – 15)

Zygaena (*Mesembrynus*) *nocturna* Ebert, 1974, Beiträge zur naturkundlichen Forschung in Südwestdeutschland 33: 164, figs. 2-6

Derivatio nominis: Nach dem Autor des nominellen Taxon „*Zygaena nocturna*" und Entdecker dieser Population am Osturan-Kuh, Günter EBERT. In Dankbarkeit für langjährige Freundschaft.

Holotypus, ♂: „Iran, e.o., Lorestan, Dorud, Golgolab Dag, 2600 m, e.p.: 7. 5. – 27. 5. 2000, A. HOFMANN cult., coll. A. HOFMANN" (später deponiert in coll. SMNK).

Paratypen: 9 ♂♂, 5 ♀♀, Daten wie Holotypus, coll. A. HOFMANN; einzelne Belegtiere (Daten wie Holotypus) in coll. J.-M. DESSE, E. DROUET, T. KEIL, J. KLIR, C. M. NAUMANN, M. NICOLLE, W. G. TREMEWAN, T. WITT (via G. REISS); 1 ♂, Prov. Lorestan, Dorud 22 km E. Dobastane 8 km E, 2300 – 2500 m, L. F., leg. A. HOFMANN & P. KAUTT, coll. A. HOFMANN; 2 ♀♀, ibidem, jedoch e.l., e.p.: 3.7.1997, coll. A. HOFMANN; 1 ♂, W-IRAN, Lorestan, Dorud 5 km SE, Saravand, "Kohyeh", 2300 m, 29. – 30. 7. 1975, L. F., leg. G. EBERT & H. FALKNER, coll. SMNK; 4 ♂♂, W-IRAN, Lorestan, Dorud, Paß S Darra-che-Gahar, "Partsche Kabud", 1. – 3. 8.1975, L. F., leg. G. EBERT & H. FALKNER, coll. SMNK.

Patagia und geschlossenes Abdominalcingulum kräftig rot. Hinterflügel zart rot, dünn beschuppt, an der Wurzel glasig, schmal schwarz umrandet ohne nennenswerte Verdickung am Apex. Vorderflügelflecken gelb, vergleichsweise groß, 1+2 und 3+4 flächig zu zwei Fleckenpaaren verbunden. Insbesondere durch die starke Annäherung von Fleck 5 an 6 unterscheiden sich die Vorkommen am Osturan-Kuh (Lorestan) recht auffällig von der nominotypischen Unterart im Kuh-e Dena – Massiv (Boyer Ahmad va Kuhgiluye). Während bei diesen Populationen aus der Umgebung von Sisakht, von Ardekan, vom Gardaneh-ye Meymand oder von Chenar Mahmoudi die Flecken 5 und 6 stets deutlich durch eine breite schwarze Fläche getrennt sind und somit dem Zeichnungsmuster von *Z. manlia* entsprechen, tendieren bei Tieren aus der Umgebung von Dorud diese beiden Endmakeln zur Ausbildung eines einzigen zusammengeflossenen Beilflecks (ca. 50 %). Nur weniger als 20 % haben oben und unten getrennte Flecken; aber auch bei diesen Tieren sind die Flecken dann stärker angenähert als bei topotypischen Tieren. Gelegentlich sind die Flecken im unteren Bereich zusammenhängend, nach oben noch durch eine dünne „kommaförmige" Einbuchtung getrennt. Diese Zeichnungsmerkmale treffen auch auf Tiere vom Kamaran-Tal (Fereydun Shahr S) zu, nicht jedoch die Färbung der Hinterflügel dieser Population. Bei ca. einem Drittel der vorliegenden Tiere (n = 18) wird die rote Grundfarbe durch orange oder gar gelbe Schuppen ersetzt. Es handelt sich hierbei um eine phänotypisch bereits abweichende, isolierte Population, die mehrheitlich ihre subspezifische Zugehörigkeit zu *eberti* subsp. nov. aber noch klar erkennen lässt.

Charakteristisch für *Z. nocturna* (und *Z. seitzi* REISS, 1938) ist bekanntermaßen die konstant unterschiedliche Färbung von Vorder- (gelb) und Hinterflügeln (rot). Während nun am Osturan-Kuh in Höhenlagen zwischen 2200 und 3000 m *Z. nocturna eberti* subsp. nov. monomorph in dieser Form auftritt, scheint in tieferen Lagen (1600 – 2000 m) des selben Massivs diese gelb/rot gefärbte Form in polychromatischen Mischpopulationen mit gelb/rot, orange/rot oder rein rot gefärbte Individuen überzugehen. Zuchtergebnisse im Freiland aufgesammelter L_1, L_2 – Räupchen (1999) sowie mehrerer Eigelege (1997) vom Duschderaz-Paß bei Dorud (HOFMANN

2000: plate III, figs. 22 - 27, 192 ff) lieferten folgende Resultate (1998 – 2000):

[n = 35]	*manlia*-artig	*cuvieri*-artig
gelb/rot (*nocturna*-artig)	1/0	0/1
orange/rot		0/2
rot/rot	6/3	14/8

Dabei gilt es zu bedenken, dass aus ein- und demselben Eigelege (1997) neben *manlia*- und *cuvieri*-artigen Individuen auch ein Tier mit gelben Vorderflügeln hervorging (HOFMANN 2000: plate II, fig. 14). Entweder findet hier im geographischen Kontaktbereich von *manlia/cuvieri* mit *Z. nocturna* eine phänoptypisch-konvergente Annäherung durch gleichgerichteten Selektionsdruck statt oder es handelt sich hierbei um Vorkommen von Hybriden zwischen *Z. nocturna* und *Z. manlia/cuvieri*. Hierfür könnte u.a. die sehr variable, von *Z. nocturna* abweichende, an *Z. manlia/cuvieri* aber bisweilen stark angenäherte Raupenzeichnung sprechen (HOFMANN 2000a: 198, fig. 2; HOFMANN 2000b: 228, fig. 8b). Auch bestärken mehrere fertile Kreuzungsexperimente (s. HOFMANN & TREMEWAN 2003: 10) diesen Verdacht. Neben den unterschiedlichen Raupenphäna wird eine befriedigende taxonomische Interpretation auch durch verschiedene Kokonfarben (weiß bei *Z. nocturna*, gelb bei durch den Zuchten vom Duschderaz-Paß) erschwert. Eine vergleichbar polymorphe „Population" fand T. KEIL 2001 (pers. Mitt.) etwas weiter nordöstlich zwischen Dorud und Khoramabad (1800 m), die allerdings phänotypisch stärker an *Z. cuvieri/Z. tamara* angenähert ist.

Zygaena (Agrumenia) magiana pamirescens subsp. nov.

(Figs. 16 – 18)

Zygaena (Agrumenia) magiana Staudinger, 1889, Stettiner entomologische Zeitung 50: 23

Derivatio nominis: Die Tiere zeigen starke habituelle Annäherung an *Zygaena (Agrumenia) pamira* Sheljuzhko, 1919.

Holotypus, ♂: „Kirghizstan, Alai mountains, Gaumich pass, H = 3.800 m, 26.07.1999, coll. A. HOFMANN" (später deponiert in coll. SMNK).

Paratypen: 31 ♂♂, 9 ♀♀, Daten wie Holotypus, coll. A. HOFMANN.

Abgesehen von einer meist nur angedeuteten rötlichen Patagia ist der Körper zeichnungslos matt schwarz. Die Vorderflügelflecken sind wohl entwickelt, Fleck 1 und 5 gelb umsäumt, rötlich gekernt, selten völlig gelb, Fleck 2 – 4 und 6 gelb, meist ohne Spuren roter Schuppen. Hinterflügel rot von schwarzer, im Analfeld ausfransender Linie umgrenzt, am Apex verbreitert. Ein ♂ lässt *magiana*-typische Zeichnung mit roten Flecken 1+2, 3 und 5 erkennen, auch Fleck 6 und 4 sind bei diesem Tier leicht rot bestäubt, ein ♀ zeigt alle Flecken rot gekernt. Der Basisfleck (1+2) ist durch den schwarz beschuppten Stamm der Radialader getrennt. Fleck 2a ist nicht entwickelt.

Von allen bekannten *Z. magiana*-Unterarten ist *Z. m. pamirescens* subsp. nov. durch ihre dominierende gelbe Vorderflügelfleckenfarbe leicht zu unterschieden. Sie kann weder mit den verdunkelten Populationen vom Kumbel-Paß (*Z. m. kumbelica* Tremewan & Naumann, 1989) noch mit den hyalinen nominotypischen Tieren oder mit den rotausgefärbten Unterarten (*Z. m. alaudina* Tremewan & Naumann, 1989, *Z. m. alaica* Holik & Sheljuzhko, 1956, *Z. m. kohistana* Grum-Grshimailo, 1893) verwechselt werden. Habituell erinnert die Mehrheit der Tiere stärker an *Z. pamira*. Beide „Arten" sind streng allopatrische Vertreter der Orealfauna Zentralasiens. Zukünftige Aufsammlungen im tadschikischen Kontaktbereich könnten mehr Klarheit bringen, wie beide Taxa zu bewerten sind. Syntopes Auftreten zweier so eng verwandter und ökologisch nahestehender Taxa ist jedoch kaum zu erwarten. Sollte sich eine klinale phänotypische Annäherung ergeben, ist von einer einzigen Biospezies auszugehen. Zuchtexperimente (Kreuzungsversuche, Anlockversuche etc.) stehen noch aus.

Aus der selben Region (Kollektorny Range, Gaumich pass, 4.8.1998) liegt eine Serie ♂♂, ♀♀ von *Z. cocandica* Erschoff, 1874, vor. Auch diese Tiere sind durch kräftigere Farbanlagen, rote Ausfärbung der Basisflecken 1+2 zu einem einzigen großen Makel und stets vorhandenes rotes Abdominalcingulum mit *Z. magiana pamirescens* subsp. nov. nicht verwechselbar. W. ECKWEILER fing 1993 in der östlichen Turkestanski-Kette (Kirgistan, Osh oblast, Ljailjak – Aksu valley, 3100 – 3500 m) einige Einzeltiere, die vermutlich zu *Z. magiana* gehören und zu *pamirescens* subsp. nov. gezogen werden könnten. Im Gegensatz zu den Tieren vom Gaumich-Pass besitzen diese 2 ♂♂, 1 ♀ jedoch ein Abdominalcingulum sowie einen zusammengeflossenen Basisfleck (1+2), wobei die Rotfärbung von Fleck 1 auch auf Fleck 2 übergreift. Fleck 2a ist angedeutet.

Zygaena (Agrumenia) formosa molleti subsp. nov.

(Figs. 25 – 27)

Zygaena (Agrumenia) formosa Herrich-Schäffer, 1852, Systematische Bearbeitung der Schmetterlinge von Europa 6: 45; 1851, ibidem 2: pl. 14, fig. 99 [non-binominal]

Derivatio nominis: Nach Bernard MOLLET (Gometz-le-Châtel). „Merci" für wertvolles Belegmaterial und zahlreiche Zuchtmitbringsel.

Holotypus, ♂: „Turkiye, prov. Niğde, Ulukişla, 2500 – 3000 m, 4.8.1995, leg. B. MOLLET", coll. A. HOFMANN (später deponiert in coll. Staatliches Museum für Naturkunde Karlsruhe).

Paratypen: 5 ♂♂, 4 ♀♀, Daten wie Holotypus, coll. A. Hofmann; 1 ♀, „Bolkar daglari N, 2000 – 3000 m, (Nigde) – Turkquie, 19-20 juillet 1998, Frédéric Carbonell leg.", coll. A. Hofmann; 50 ♂♂, 30 ♀♀, „Southern Turkey, Prov. Konya, Bolkar dagları, Aydos dağı, NE side, 37°20' N, 34°24' E, 2700 m, 23.VII.1998, C. u. A. Naumann leg.", coll. C. M. Naumann; 1 ♂, 2 ♀♀, „Turkey, Niğde, 3100 m, Bolkar daglari, N side, SW Maden, 28.VII.1994, H. v. Oorschot, H. v.d. Brink, H. v.d. Poorten, W. de Prins [leg.]", coll. C. M. Naumann; ibidem, 1 ♀, 30.VII.1997, W. de Prins, A. Olivier, H. v.d. Poorten, [leg.]", coll. C. M. Naumann.

Habituell und ökologisch scheint *Z. f. molleti* subsp. nov. zwischen *Z. formosa* Herrich-Schäffer, 1852 und *Z. peschmerga* Eckweiler & Görgner, 1981 zu stehen. Insbesondere das tristere Rot und die verkleinerten Vorderflügelflecken sowie das Fehlen von Fleck 2a erinnern stark an *Z. peschmerga*. Der Nierenfleck tendiert wesentlich stärker zur Loslösung von Fleck 5 als dies bei anderen *Z. formosa*-Populationen festzustellen ist. Die Flecken sind klein, insgesamt jedoch größer als bei *Z. peschmerga*, der Abstand zwischen dem Basisfleck 1+2 und Fleck 3 ist flächiger, 3+4 sind fast immer durch die Weißumrandung verbunden, ebenso kontaktiert Fleck 5 mit dem Fleckenpaar 3+4. Die Basisflecken 1+2 sind zu einer einzigen Makel verschmolzen, die im Gegensatz zu *Z. peschmerga* auch nicht andeutungsweise durch schwarze Schuppen auf der Radialader getrennt ist. Die Patagia ist nur bei den ♀♀ rötlich, bei den ♂♂ weißlich-grau oder bräunlich. 2 ♀♀ zeigen oberseits ein schwach ausgeprägtes einfaches Abdominalcingulum, bei den anderen beiden ♀♀ ist der Gürtel nur unterseits in Spuren zu erkennen. Die ♂♂ sind uncinguliert.

Das Vorkommen einer gut differenzierten hochmontan-alpinen *formosa*-Population in der Dornpolsterstufe am Bolkar Dağ darf durchaus als überraschend bezeichnet werden. Im selben Gebiet (Ulukişla 11 km E) fliegt nämlich zur gleichen Zeit auf 1100 – 1200 m Höhe eine völlig normal aussehende *Z. formosa*-Population mit großen leuchtend roten Flecken, roter Patagia, zwei- bis dreifachem Abdominalcingulum und wohl entwickeltem Fleck 2a. Auch das Auffinden einer weiteren – phänotypisch fast identischen – Hochgebirgspopulation mehr als 500 km (Luftlinie) weiter nordöstlich in der Prov. Erzincan („Turquie, Erzincan, Mercan Daglari, N 39°35'-E 39°29', 3100 m, 27.VII. 1999, Dominique Dumont leg.", 1 ♂, 1 ♀, weiteres Belegmaterial in coll. D. Dumont) könnte bei besserer Kenntnis der ökologisch-biologischen Eigentümlichkeiten Anlass sein, die Eigenständigkeit bzw. Zugehörigkeit von *Z. f. molleti* subsp. nov. neu zu diskutieren. Klärungsbedarf besteht weiter hinsichtlich *Z. formosa kotzschi* Reiss, 1935. Diese Unterart wurde aus der Geröllschuttzone nahe der armenischen Grenze oberhalb 3000 m beschrieben. Sie zeigt Fleckenreduktion, lässt aber noch wesentlich klarer (rotes Cingulum, rote Patagia etc.) ihre Zugehörigkeit zu *Z. formosa* erkennen.

Z. formosa molleti subsp. nov. (2600 – 3000 m) ist am Bolkar Dag etwas höher eingenischt als *Zygaena (Zygaena) loti senilis* Burgeff, 1914 (Tremewan & Tarmann 2003) und die zeitgleich fliegende *Adscita capitalis* (Staudinger, 1879), die 2600 m Höhe nicht wesentlich zu überschreiten scheint (B. Mollet, pers. Mitt.). Die Falter fliegen auffallend niedrig über dem Grund, eine Anpassung an die häufigen, teilweise recht heftigen Winde. Als Raupennahrungspflanze konnte eine rotblühende, flachliegende bis kriechende, nichtstachelige Fabaceae ausgemacht werden. Eine Eiablage in die Mittelrispe der auffällig stark behaarten Fiederblätter konnte von B. Mollet beobachtet werden.

Zygaena (Agrumenia) tenhagenova sp. nov.

(Figs. 31, 32)

Derivatio nominis: Dem Entdecker Dr. Wolfgang ten Hagen in Anerkennung seiner verdienstvollen Feldarbeit (1996 – 2003) für die Erforschung der iranischen Zygaenenfauna gewidmet. Das Art-Epitheton ist ein Substantiv in Apposition, da der Name *tenhageni* bereits für *Zygaena rubricollis tenhageni* Hofmann & Tremewan, 2003 vergeben ist.

Holotypus, ♂: „Iran, Kordestan, Paß NE Baneh, (Ostseite); 1900 – 2100 m, 16. VI. 2001, leg. [W.] ten Hagen ", coll. A. Hofmann (später deponiert in coll. SMNK).

Paratypus: 1 ♂, Daten wie Holotypus, coll. A. Hofmann. ♀ noch unbekannt.

Die habituelle Übereinstimmung beider Tiere zeigt, dass hier eine eigenständige, zweifelsfrei beschreibenswerte Population vorliegt. Einige Merkmale und Merkmalskombinationen sind als taxonomische Besonderheiten hervorzuheben: Gelbe Halskrause (Patagia) bei rotem Abdominalcingulum (auf zwei Segmenten), hell-ockergelbe Beine, Vorderflügelflecken 2, 3, 4 und 6 gelb, Fleck 1 entlang der Costa rot, Fleck 5 rot gekernt, Fleck 2a rot bepudert; Fleck 4 nahezu quadratisch. Hinterflügelumrandung schmal, am Apex verstärkt, mit auffälliger Verdickung („Zahn") am beginnenden Analfeld; ein fast unbeschupptes, somit durchsichtiges Feldchen durchzieht die roten Hinterflügel von der Flügelwurzel fast bis zur schwarzen Analfeldverdickung reichend.

Die beiden einzigen bislang bekannten Tiere erlauben keine endgültige Entscheidung, ob es sich um eine wohldifferenzierte Biospezies oder „nur" um eine außergewöhnliche Subspezies von *Z. chirazica* Reiss, 1938, oder *Z. naumanni* Hille & Keil, 2000, handelt. Eine Beschreibung als Unterart von *Z. chirazica* wären jedoch nur möglich gewesen, wenn gleichzeitig die geographisch dazwischen siedelnde *Z. naumanni* synonymisiert worden wäre. Dieser Schritt sollte jedoch erst vollzogen werden, wenn weitere gut begründete Argumente (Larvalbiologie, Pheromone, DNA, Kreuzungs- und Anlockexperimente) vorliegen.

Habituelle Unterschiede zu diesen beiden Taxa, die den üblichen Rahmen einer Subspezies übertreffen, sind nicht zu übersehen. Insbesondere der ausgeprägte hyaline Wisch auf den Hinterflügeln von der Flügelwurzel bis zum „Zahn" der Umsäumung stellt eine eigenartige Besonderheit dar, die in dieser Form bei keiner anderen *Z. chirazica*-Unterart einschließlich *Z. naumanni* auftritt. Vielmehr erinnert diese Merkmalskombination („schwarzer Zahn – hyaliner Wisch") eher an *Z. escalerai* Poujade, 1900, (etwa aus Dorud oder Sibak) zu der auch weitere Ähnlichkeiten bestehen, so z. B. die unterschiedliche Vorder- (gelb) und Hinterflügelfärbung (rot). Die Mehrzahl signifikanter Merkmale (zweifaches Abdominalcingulum, Ausgestaltung und Anhängung der beiden Vorderflügelflecken 5+6 etc.) lässt jedoch eine nähere Verwandtschaft mit *Z. chirazica/naumanni* vermuten.

Die nächsten bekannten Vorkommen von *Z. naumanni* sind ca. 500 km weiter südöstlich gelegen, dazwischen sind bislang keine Populationen bekannt geworden. *Z. chirazica* hat ihre nächsten Fundorte bei Semirom und Meymand (ca. 730 km Luftlinie entfernt).

Am Locus typicus zwischen Baneh und Saqez unweit der irakischen Grenze fliegt die neue Art zusammen mit *Z. tamara* Christoph, 1889, und *Z. cuvieri* Boisduval, [1828]. Die habituelle Ähnlichkeit mit der syntopen *Z. tamara* (anderes Subgenus!) ist nicht zu übersehen (vgl. Abbildungen). Sie tritt hier in der gleichen zweifarbigen Form („mahabadicoid") mit gelber Patagia, gelben Vorder- und roten Hinterflügeln auf.

Zygaena (Agrumenia) haberhaueri demangei subsp. nov.

(Figs. 34 – 39)

Zygaena (*Agrumenia*) *haberhaueri* Lederer, 1870, Annales de la Societé entomologique de Belge 13 (1869-70): 29, 45

Derivatio nominis: Für Jacques DEMANGE (Denis du Val), dem wir die Entdeckung der am stärksten abweichenden Population dieser Unterart verdanken.

Holotypus, ♂: „Iran prov. Azerbaijan E, Kandovan 2350m, 37°N47,063 46°E15,689, 18-20 VII 2000, J&M DEM[ANGE leg.]"; coll. A. HOFMANN (später deponiert in coll. SMNK).

Paratypen: 7 ♂♂, 3 ♀♀, Daten wie Holotypus, coll. A. HOFMANN; weitere Paratypen (Daten wie Holotypus) coll. J. DEMANGE.

Von der nominotypischen Unterart und allen nachfolgend beschriebenen hierzu gehörigen Taxa unterscheidet sich *Z. h. demangei* subsp. nov. durch auffällig große, kräftig weiß umsäumte Vorderflügelflecken und ein gut entwickeltes rotes Abdominalcingulum (meistens über 2-3 Segmente). Eine rote Halskrause ist stets vorhanden, ♀♀ besitzen zumindest andeutungsweise rote Tegulae. Diese Schönheitsmerkmale erinnern an *Z. olivieri* Boisduval, [1828], von der sich *Z. h. demangei* subsp. nov. jedoch deutlich durch ihren *haberhaueri*-typischen, kälteren Rotton abhebt. Die Vorderflügelflecken 1+2 und 5+6 sind paarweise im Rot verbunden, Fleck 3+4 werden nicht selten durch weiße Schuppen getrennt. Entlang der Costa der Vorderflügel zieht sich ein Wisch weißer Schuppen. Am stärksten ist diese Ausprägung bei Tieren von der Typenlokalität zu erkennen. Individuen aus Hamadan sind zwar ebenfalls noch durchwegs cinguliert, häufig jedoch nur auf einem oder zwei Segmenten. Die roten Tegulae bei den ♀♀ sind auf wenige Schuppen reduziert. Unweit Zanjan treten dann die ersten uncingulierten Individuen hinzu (ca. 5 %). Die Flecken werden kleiner, die prominente Weißumrandung schmäler. *Z. h. haberhaueri* und *Z. h. elbursica* TREMEWAN, 1975, sind uncinguliert (ca. 90 %), durch ihre kleineren Vorderflügelflecken und schwächer ausgeprägte Weißumsäumung nicht mit *Z. h. demangei* subsp. nov. verwechselbar. *Z. haberhaueri optima* Reiss, 1939 , ist ebenfalls uncinguliert und besitzt darüber hinaus ein weißes Collar.

Z. haberhaueri demangei subsp. nov. besiedelt ein vergleichsweise großes Areal in Nordwestiran. Eindeutig hierzu gehöriges Vergleichsmaterial liegt aus den Provinzen Azarbaygan-e Sharqi (Kuh-e Sahand, Talish, Kalaybar), Zanjan und Hamadan (Gardaneh-ye Avaj) vor. Auch Tiere weiter nordwestlich anschließender Regionen (Buzgov/Nachitschevan, Talysh/Republik Azarbeidjian) besitzen – wenngleich etwas abgeschwächt – eindeutig hierher verweisende Merkmalszüge (Cingulum, weiße Fleckenumrandung).

Zygaena (Zygaena) viciae pelopis subsp. nov.

(Figs. 46 – 48)

Zygaena (*Zygaena*) *viciae* [Denis & Schiffermüller], 1775, Ankündung eines systematischen Werkes von den Schmetterlingen der Wienergegend: 45 (*Sphinx*)

Derivatio nominis: Nach Pelops, Gestalt der griechischen Mythologie, mächtigster König der Insel, die von ihm den Namen erhält. „Peloponnesos": Insel des Pelops.

Holotypus, ♂: „HELLAS/Peloponnes, Aroania-Oros, Chelmos, Kalavrita 1600 m, 5.-21.VII.1987, H.

ARHEILGER [leg.]“; coll. A. HOFMANN (später deponiert in coll. SMNK).

Paratypen: 1 ♀, Datum wie Holotypus, coll A. HOFMANN; ibidem, 5 ♂♂, 1 ♀, coll. H. ARHEILGER; ibidem, 8 ♂♂, 4 ♀♀, 1300 m, 15. – 22. VI. 1987, coll. H. ARHEILGER; ibidem 1 ♂, „T. ARHEILGER [leg.]“, coll. H. ARHEILGER; ibidem 1 ♂, „1750 m, 5. – 21. VII. 1987, H. ARHEILGER“ [leg.]; 1 ♀, „ Griechenland, Peloponnissos, Aroania Ori, Umgebung Kalavryta, 20.6.1976“, leg. J. WOLF; ibidem 1 ♂, 28.6.1976; ibidem 1 ♀, 24.6.1986; 1 ♂, „ Griechenland, Peloponnissos, Erymanthos Óros, 1500 m, 29.6.1990, leg. J. WOLF; 1 ♂, „Graecia mer., Peloponnes sept., 7.6.1976, Trikala, 1400 m, leg. K. BERNHAUER“, ex coll. G. REISS, coll. A. HOFMANN; 1 ♂, „Greece, Prov. Ahaia, versant nord du mont Chelmos, 1450/1650 m, 3/VII/1996, Dominque DUMONT leg.“.

Z. viciae pelopis subsp. nov. zeichnet sich durch schmale, spitze Vorderflügel und habituelle Annäherung an *Z. filipendulae* aus. Die Tiere sind groß, im Durchschnitt sogar größer als syntope *Z. filipendulae*. Ein Abdominalcingulum fehlt stets. Die Vorderflügelflecken 1+2 und 5+6 sind paarweise verbunden, 3+4 werden von schwarzen Setae getrennt. Fleck 5 hängt abgewinkelt an Fleck 6 (ähnlich *Z. graslini* Lederer, 1855). Fleck 6 ist verkleinert; nur bei einem einzigen von 25 vorliegenden Tieren fehlt diese Endmakel. Die Rotfärbung ist vergleichsweise trist, keinesfalls leuchtend oder orangefarben. Die *Z. viciae*-typische Hinterflügelumsäumung ist am Apex und im Analfeld erweitert. Dieses Merkmal in Kombination mit dem winzigen Fleck 3 erlaubt eine sichere habituelle Unterscheidung von *Z. filipendulae*. Im Vergleich mit anderen *Z. viciae*-Unterarten zeigt *Z. v. pelopis* subsp. nov. gewisse Ähnlichkeiten mit *Z. v. amanica* Reiss, 1935 vom Nurudağ Geçidi unweit der türkisch-syrischen Grenze. Die geographisch nächststehenden Unterarten *Z. viciae silbernageli* Reiss, 1943 und *Z. v. bosniensis* Reiss, 1922 sind fast ausnahmslos 5-fleckig. Sie sind dichter beschuppt mit wesentlich wärmerem Rotton und breiteren Vorderflügeln. Dies trifft auch für mazedonische (Ochird- u. Prespan-See vic.) und nordgriechische Populationen (Kalambaka, Katara, Pilion etc.) zu. Abdominalberingung tritt hier gelegentlich auf.

Zygaena (Zygaena) filipendulae wiegelorum subsp. nov.

(Figs. 52 – 54)
Zygaena (*Zygaena*) *filipendulae* (Linnaeus, 1758), Systema Naturae, ed. X, 1: 494 (*Sphinx*)

Derivatio nominis: Dem Ehepaar Dr. Karl-Heinz und Charlotte WIEGEL in Anerkennung seiner Verdienste um die Erforschung der Biologie mehrerer *Zygaena*-Arten gewidmet.

Als Autoren dieses Taxon zeichnen A. HOFMANN und W. G. TREMEWAN verantwortlich

Holotypus ♀, „Turkey: Erzurum, Aşkale (7 km SW.), 2000 m. 20.vii.1999“ leg. et coll. W. G. TREMEWAN (später deponiert in coll. Staatliches Museum für Naturkunde Stuttgart)

Paratypen: 8 ♂♂, 8 ♀♀, „Turkey: Erzurum, Aşkale (7 km SW.), 2000 m. ab ovo, 27.iii.–8.iv.2000. W. G. & S. M. TREMEWAN“, coll W.G. TREMEWAN; 1 ♂, „Türkei, Erzurum, 20 km nördl. Askale, Kop Gec., 1700 m, 19.7.1992, leg. G. BAISCH”, coll. A. HOFMANN; 1 ♂, ibidem, 2300 m, 29.7.1992; 2 ♂♂, „Türkei, n. Askale, Kopdag, 2000 m, Tasagil, Weideland/Mähwiesen, 7.7.1997, J. U. MEINEKE leg.“, coll. A. HOFMANN; 2 ♂♂, „Türkei, Bayburt, Nördl. Kop. Gec., 2100 m, 8.7.1996, leg. W. TEN HAGEN“, coll. A. HOFMANN; 4 ♂♂, „Turkey, Erzurum, Kop. gec., 2370 m, 40.01.40N, 40.31 E, 17.7.1996, K. SPATENKA lgt.“, coll. A. HOFMANN; ibidem, 4 ♂♂, 1 ♀, coll. C.M. NAUMANN; 2 ♂♂, „Kop-gecidi, 2350 m, 29.7.77, loc. 50, leg. S. WAGENER, coll. C.M. NAUMANN.

Zu *Z. f. wiegelorum* subsp. nov. gehören ferner zahlreiche weitere Vorkommen – so vom Palandöken Dağ (Erzurum SE), den Munzur und Mercan Daglari, aus der Umgebung von Ovaçik (Erzurum) und Yusufeli sowie vom Buğlan Geçidi (Bingöl – Mus) – die wir jedoch nicht als Paratypen werten.

Z. filipendulae wiegelorum subsp. nov. ist die am stärksten rotkonfluente Unterart. Sie stellt insofern das extreme Gegenstück zu den melanistischen Unterarten *Z. f. gigantea* Rocci, 1913 und *Z. f. himmighofeni* Burgeff, 1926 dar. Die 6 Vorderflügelflecken sind paarweise so miteinander verbunden, dass sie nur noch als 3 einzelne Großmakel auszumachen sind. Bei den vorliegenden Tieren vom Locus typicus geht diese Tendenz noch weiter: Ein durchgehender roter Striemen von Fleck 2 nach 4 und weiter nach 5+6 verbindet alle Flecken zu einem geradezu neuen Phänotypus. Bei einigen Männchen sind die Makel flächig auch entlang des Vorderflügelaußenrandes verbunden; solche Tiere erinnern stärker an kräftig beschuppte *Z. purpuralis* als an *Z. filipendulae*. Der Hinterflügelsaum ist sehr schmal.

Z. filipendulae wiegelorum subsp. nov. besiedelt ein relativ großes Areal vom Buğlan Geçidi im Süden (Prov. Bingöl) bis Erzurum und Bayburt (Prov. Gümüshane) im Norden. Auch ein einzelnes vorliegendes Weibchen von Yusufeli (Prov. Coruh/Artvin) sowie Tiere aus den Rize daglari und aus der Umgebung von Gümüshane scheinen hierher zu gehören. Nach Nordwesten und Osten schließen sich hiervon völlig abweichende, normal aussehende *Z. filipendulae* – Populationen an (*Z. f. tirabzonica* Koch, 1942 und *Z. f. kulpiensis* Reiss, 1935). Nur die im Südosten kontaktierenden *Z. filipendulae* *schuberti* Reiss & Reiss, 1973 vom Van-See-Gebiet tendieren bereits zur Fleckenverschmelzung. Hier sind die Vorderflügelflecken oft paarweise angenähert oder verschmolzen, meistens jedoch noch deutlich als Einzelmakel zu erkennen. Größerflächige Konfluenz hin zu *Z. purpuralis*-artigen Tieren tritt bei *Z. f. schuberti* nicht auf.

Erythristische Populationen/Unterarten sind aus der Osttürkei auch von *Z. brizae*, *Z. purpuralis*, *Z. olivieri* (Naumann & Hofmann, in Vorbereitung) und *Z. loti* (*latifa* Naumann & Naumann, 1978) bekannt. Dabei fällt auf, dass mehrere Arten gerade in der Provinz Erzurum zur Verstärkung der roten Zeichnungsanlagen tendieren (*Z. purpuralis*, *Z. olivieri*, *Z. carniolica* etc.) und mindestens 2 Arten (*Z. loti* und *Z. filipendulae*) hier ihre extremsten roten Unterarten hervorgebracht haben.

Zygaena (Zygaena) lonicerae pseudangelicae subsp. nov.

(Figs. 55 – 57)

Zygaena (*Zygaena*) *lonicerae* (Scheven, 1777), Naturforscher, Halle 10: 97 (*Sphinx*)

Derivatio nominis: Ostanatolische Populationen von *Z. lonicerae* (Scheven, 1777) zwischen Buğlan Geçidi und Van-See zeigen starke habituelle Anklänge an *Z. angelicae* Ochsenheimer, 1808.

Holotypus, ♂: „Türkei or., Prov. Van, Kuzgunkiran Gecidi, 1900 m, 19. – 23. 7. 1981, Groß, Herbst, R. & A. Hfm.", coll. A. Hofmann (später deponiert in coll. Staatliches Museum für Naturkunde Karlsruhe).

Paratypen: 1 ♀, Datum wie Holotypus; ibidem, 4 ♂♂, 14.7.1982, P. Strauß & A. Hofmann leg., coll. A. Hofmann; 2 ♂♂, „15 km östl. Tatvan, 1800 – 1900 m, 16.7.1986, leg. K. Schurian, Coll. Nr. 215", coll. A. Hofmann; 6 ♂♂, 9 ♀♀,“Asia min., Kurdistan, Van-See-Gebiet, Bitlis Vill., 20 km östl. Tatvan, 1750 m, 10. – 12. 7. 68, feuchte Wiesen, leg. Mittendorf", coll. C. M. Naumann; ibidem, 3 ♂♂, 2 ♀♀, coll. A. Hofmann via coll. C.M. Naumann.

Zu *Z. l. pseudangelicae* subsp. nov. gehören ferner die Aufsammlungen vom Buğlan Geçidi (die ich jedoch nicht als Paratypen werte): 1 ♀, „Prov. Mus, Buglan Gecidi, 1600 m, 28.6. – 4.7. 1977, leg. Holzschuh & Ressl", coll. A. Hofmann; ibidem, 1 ♂, „Bingöl/Mus, Buglan Gecidi, 1650 – 1750 m, 03.07.1986, A. Hofmann & G. & S. Reiss", coll. T. Witt (via coll. G. Reiss); 1 ♀, “Türkei, Prov. Bingöl, Buglan gec., 1600 m, 26.VI.82, leg. W. Thomas", coll. C. M. Naumann.

Neben der geringen Größe unterscheiden sich die zierlichen Tiere recht augenfällig von allen anderen *Z. lonicerae*-Unterarten durch leuchtend orangerote Färbung, vergleichsweise dünne Fühler und kleine, fast runde Vorderflügelflecken 3, 4 und 5. Die schwarze Hinterflügelumsäumung ist im Analbereich sehr schmal, vom Cupido bis zum Apex mäßig verstärkt. Insgesamt erinnern die Tiere stark an *Z. angelicae*.

Die eurosibirisch verbreitete Art, *Z. lonicerae,* gehört in Zentralanatolien zu den großen Seltenheiten. Während das Areal der nordanatolischen und armenischen *Z. lonicerae*-Populationen (subsp. *abbastumana* Reiss, 1922) im pontischen Waldgürtel liegt, wo die Art auch flächenhaft verbreitet ist, besiedelt *Z. l. pseudangelicae* subsp. nov. nur sehr kleinräumige, heute größtenteils waldfreie Lebensräume des östlichen Zentralanatolien. Die Biotope am Buğlan und Kuzgunkiran Geçidi sind azonale, mesophile Kleinbiotope in der subalpinen Grassteppe, stellenweise Mähwiesen (Mahd ab Anfang, Mitte Juli), in ihren Randbereichen oft von lichtem Eichenbuschwald durchsetzt. In diesem ökologisch besonders reich strukturierten Raum überlagern sich rezent die Areale zahlreicher arborealer und eremialer Arten und bedingen so eine besonders hohe Artendiversität. *Z. lonicerae* tritt hier syntop mit *Z. cuvieri* Boisduval, [1828], *Z. cambysea* Lederer, 1870, *Z. purpuralis* (Brünnich, 1763), *Z. minos* ([Denis & Schiffermüller], 1775), *Z . olivieri* Boisduval, [1828], *Z. sedi* Fabricius, 1787, *Z. carniolica* (Scopoli, 1763), *Z. loti* ([Denis & Schiffermüller], 1775), *Z. viciae* ([Denis & Schiffermüller], 1775), *Z. dorycnii* Ochsenheimer, 1808 und *Z. filipendulae* (Linnaeus, 1758) auf. In der näheren Umgebung sind weitere Arten (*Z. manlia* Lederer, 1870, *Z. rubricollis* Hampson, 1900, *Z. tamara* Christoph, 1889, *Z. punctum* Ochsenheimer, 1808, *Z. brizae* (Esper, 1800), *Z. osterodensis* Reiss, 1921, *Z. peschmerga* Eckweiler & Görgner, 1981) anzutreffen, so dass in türkisch Kurdistan zwischen Buğlan Geçidi und Van-See-Gebiet mit 19 Arten ein rezentes Mannigfaltigkeitszentrum der Gattung *Zygaena* erreicht sein dürfte. Für *Z. lonicerae* bilden diese Nachweise zugleich ihre südöstliche Arealgrenze.

Danksagung. Beiträge zum Gelingen dieser Arbeit haben beigesteuert: H. Arheilger, T. Arheilger, G. Baisch, F. Carbonell, J.-M. Desse, J. Demange, D. Dumont, G. Ebert, Dr. W. Eckweiler, G. Flutsch, J. J. de Freina, Dr. A. Kallies, H. u. P. Kautt, T. Keil, R. Leestmans, Dr. J.-U. Meineke, B. Mollet, M. Nicolle, Prof. Dr. C. M. Naumann (†), Dr. G. Reiss (†), Dr. K. Schurian, Dr. G. Tarmann, Dr. K. Špatenka, M. Ströhle, Dr. W. ten Hagen, Dr. W. G. Tremewan und J.-C. Weiss. Ihnen allen bin ich einmal mehr sehr zu Dank verpflichtet.

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1-3: *Zygaena* (*Mesembrynus*) *rubricollis arachosica* n. subsp.; 1: Holotypus, ♂, 31 mm: „Pakistan, Baluchistan, Quetta/Urak, 2400 – 2700 m, 24. – 26.V.83, leg. ECKWEILER“; 2: Paratypus, ♂, 36 mm: Daten wie Holotypus jedoch 23. – 24.V. 1979; 3: Paratypus, ♀, 34 mm: ibidem.

4-6: *Zygaena* (*Mesembrynus*) *rubricollis rubricollis* Hamspon, 1900; 4: Topotypus, ♂, 34 mm: "Pakistan, Chitral, Birmoglasht, 2700 - 2900 m, 6. VII.83, leg. ECKWEILER“; 5: Topotypus, ♂, 32 mm: „Chitral, 2800 - 3000 m, Birmoglasht, Chagh Bini, Pakistan, 30-VI-97, [leg.] MARC NICOLLE”; 6: Topotypus, ♀, 33 mm: Daten wie fig. 4 jedoch 29. VI.83.

7: *Zygaena* (*Mesembrynus*) *rubricollis shahkuhica* n. subsp.; Holotypus, ♂, 30 mm: „Iran, prov. Mazandaran, Shah Kuh (Est), versant nord, 2800 – 3000 m, N36°32-E54°26, 15/17-VII-1998, [B.] MOLLET leg.“.

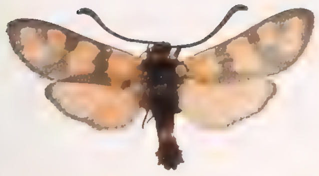
8: *Zygaena* (*Mesembrynus*) *manlia manlia* Lederer, 1870: ♂, 30 mm: „Iran, prov. Mazandaran, Shah Kuh (Est), versant nord, 2800 – 3000 m, N36°32-E54°26, 17/19-VI-2000, G. FLUTSCH & B. MOLLET leg.“.

9: *Zygaena* (*Mesembrynus*) *cacuminum* Christoph, 1877; Topotypus, ♂, 31mm: Iran, Mazandaran, Shah Kuh, Sharud S, Shah Kuh-e Pa'in vic., 2700 – 2900 m, 19. – 21. 7. 1999, A. HOFMANN, B. MOLLET & J.U. MEINEKE leg.”.

10-12: *Zygaena* (*Mesembrynus*) *nocturna nocturna* Ebert, 1974; 10: Paratypus, ♂, 33 mm: “[Iran], Fars, 50 km NW Ardekan, Tange Surkh, 2250 m, 16.6.1972, EBERT/PAZOUKI leg. “; 11: ♂, 34 mm: „Iran, L. F., Prov. Boyer Ahmad-va-Kohgiluyeh, Gardaneh Meymand, 2450 – 2800 m, 15. – 17.6.2001, J.U. MEINEKE & A. HOFMANN leg.“; 12: ♂, 31 mm: „Iran, e.o., Chaharmahal-va-B., Borujen S, Gardaneh-ye Chenar Mahmoudi S, e.p.: 22.4. – 8.6.2002, A. HOFMANN cult.“.

13-15: *Zygaena* (*Mesembrynus*) *nocturna eberti* n. subsp.; 13: Holotypus, ♂, 32 mm: Iran, e.o., Lorestan, Dorud, Golgolab Dag, 2600 m, e.p.: 7.5. – 27.5. 2000, A. HOFMANN cult.“; 14: Paratypus, ♂, 32 mm: Daten wie Holotypus; 15: ♂, 33 mm: „Iran, e.p., Prov. Esfahan, Fereydun Shahr S, Kamaran vic., 2700 – 2800 m, e.p.: 29.6.2001, A. HOFMANN & J.U. MEINEKE leg.“.

16-18: *Zygaena* (*Agrumenia*) *magiana pamirescens* n. subsp.; 16: Holotypus, ♂, 26 mm: “Kirghizstan, Alai mountains, Gaumish pass, H = 3.600m, 26.07. 1999, coll. A. HOFMANN“; 17: Paratypus, ♂, 25 mm, Daten wie Holotypus; 18: Paratypus, ♀, 27 mm, ibidem.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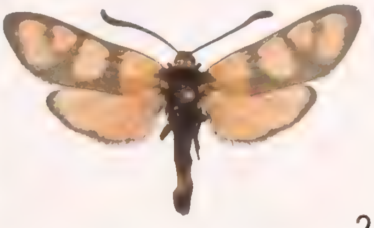
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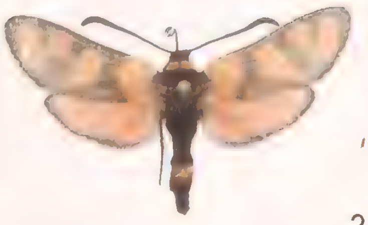
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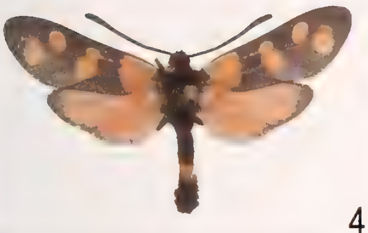
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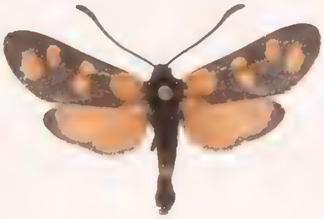
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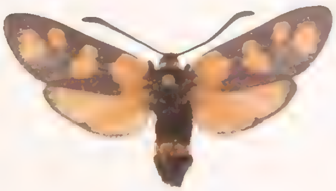
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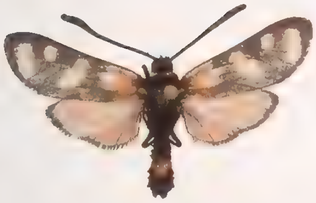
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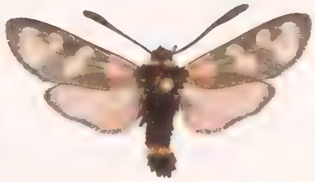
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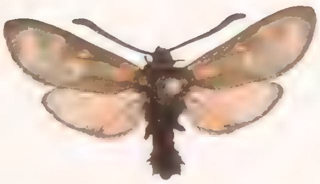
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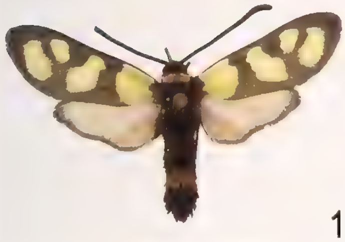
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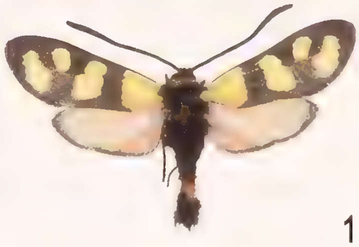
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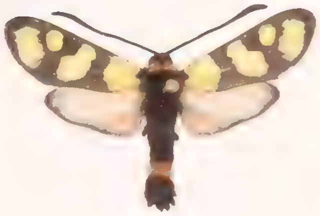
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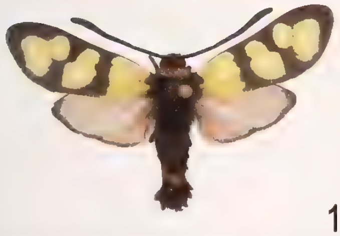
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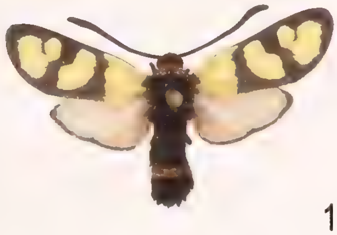
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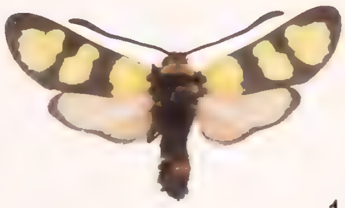
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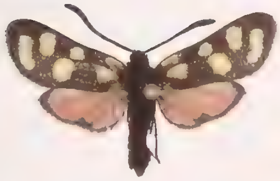
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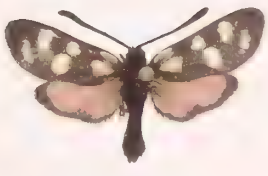
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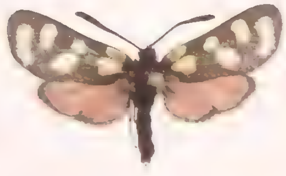
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19: *Zygaena* (*Agrumenia*) *magiana magiana* Staudinger, 1889: ♂, 26 mm: "Turkestan"

20: *Zygaena* (*Agrumenia*) *magiana alaica* Holik & Sheljuzhko, 1956: ♂, 27 mm: "UdSSR, Kirghisistan, Alai-Geb., Kaindy b. Ferghana, 3000 – 3500 m, 10.-20.7. 1986, Coll. Dr. A. SCHULTE, coll. A. HOFMANN".

21: *Zygaena* (*Agrumenia*) *magiana alaudina* Tremewan & Naumann, 1989: Topotypus, ♂, 24 mm: "N. Tajikistan, Zerevshan, Fanskiye Gory, Alaudin Lakes, 3.600 m, 29. VII. 1997, leg. G. LUTSENKO, ex coll. C.M. NAUMANN, coll. A. HOFMANN".

22-24: *Zygaena* (*Agrumenia*) *cocandica* ad *cocandica* Erschoff, 1874: "Kirgiztan, Alai, Kollectorniy Range, Gaumich Pass, 4.8.1998, coll. A. HOFMANN."; 22: ♂, 24 mm; 23: ♂, 24 mm; 24: ♀, 26 mm.

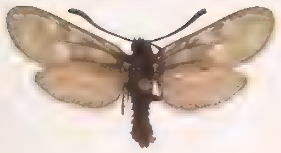
25-27: *Zygaena* (*Agrumenia*) *formosa molleti* n. subsp.; 25: Holotypus, ♂, 24 mm: "Turkiye, prov. Nigde, Ulukisla, 2500 – 3000 m, 4-VIII-1995, MOLLET B. leg."; 26: Paratypus, ♂, 25 mm, Daten wie Holotypus; 27: Paratypus, ♀, 26 mm, ibidem.

28-30: *Zygaena* (*Agrumenia*) *formosa malatiana* Rebel, 1901; 28: ♂, 23 mm: "Türkei centr., Sivas 10 – 14 km S, 1350 m, 15./16.7.1986, A. HOFM., G. & ST. REISS"; 29: ♂, 23 mm: "Türkei mer., Nigde S, Ulukisla 11 km E, Hasangazi vic., 1160 m, 14.7.1986, A. HOFM., G. & ST. REISS"; 30: ♀, 26 mm: Daten wie fig. 29.

31, 32: *Zygaena* (*Agrumenia*) *tenhagenova* n. spec.; 31: Holotypus, ♂, 26 mm: "Iran, Kordestan, Paß NE Baneh (Ostseite), 1900 – 2100 m, 16.VI. 2001, leg. TEN HAGEN"; 32: Paratypus, ♂, 26 mm, Daten wie Holotypus.

33: *Zygaena* (*Mesembrynus*) *tamara mahabadica* Reiss, 1978; ♂, 27 mm, Daten wie fig. 31.

34-39: *Zygaena* (*Agrumenia*) *haberhaueri demangei* n. subsp.; 34: Holotypus, ♂, 27 mm: "Iran, prov. Azerbaijan E, Kandovan, 2350 m, 37°N47,063 46°E15,689, 18-20 VII. 2000, J & M DEM[ANGE]"; 35: Paratypus, ♂, 27 mm, Daten wie Holotypus; 36: Paratypus, ♀, 30 mm, Daten wie Holotypus; 37: ♂, 28 mm: „Iran, Prov. Hamadan, Hamadan NNE, Razan N, Gardanye Avaj, 2300 – 2400 m, 19. 06. 1998, A. HOFMANN/J.-U. MEINEKE [leg.]"; 38: ♀, 33 mm: „Iran, Zanjan, 25 km SW Zanjan (Pass), 1900 – 2000 m, 4. VII. 2003, leg. ECKWEILER • 890"; 39: : ♀, 30 mm: „Iran, Prov. Zanjan, Zanjan – Gilvan, Gargovol Dag, 1. Paß, ca. 1 km N. des Passes, 2400 – 2500 m, 26.6. 2001, A. HOFMANN & J.U. MEINEKE leg. „.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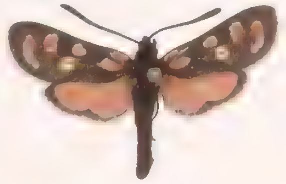
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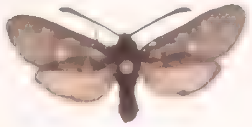
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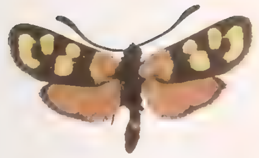
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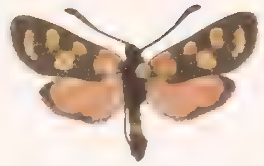
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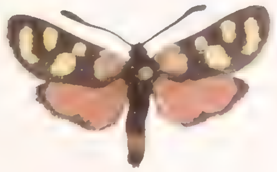
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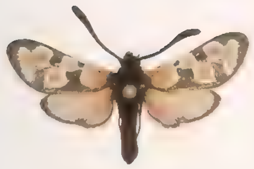
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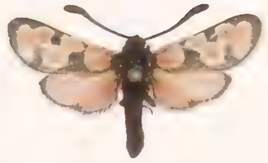
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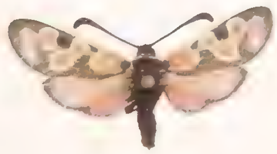
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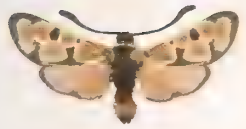
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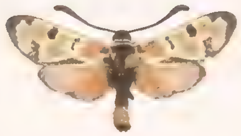
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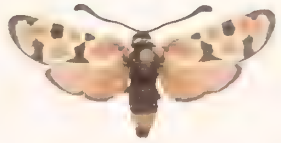
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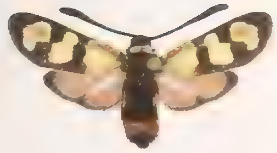
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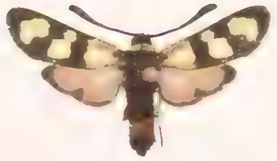
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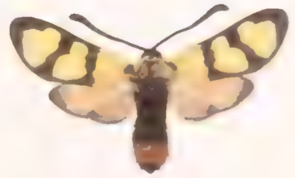
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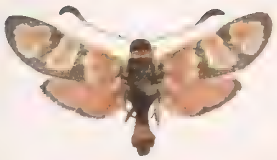
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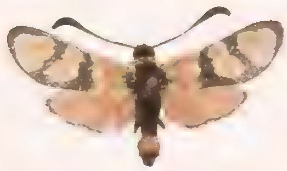
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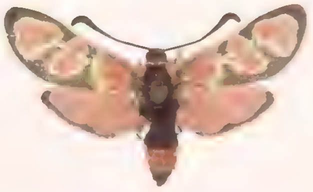
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40, 41: *Zygaena* (*Agrumenia*) *chirazica eckweileri* Naumann & Naumann, 1980; 40: Paratypus, ♂, 22 mm: “S-Iran, Kerman, Bam/ Deh Bakri, 2000 – 2500 m, 23. – 25.V. 78, leg. ECKWEILER“, ex coll. C.M. NAUMANN; 41: Topotypus, ♀, 24 mm : „Iran, Prov. Kerman, Bam W, Dehbakri 1 km S, 2200 m, 1.6. 1997, (26/97), A. HOFMANN & P. KAUTT [leg.]“.

42, 43: *Zygaena* (*Agrumenia*) *chirazica chirazica* Reiss, 1938; 42: ♂, 24 mm: “Südiran, Dasht-e-Arjan, 2000 – 2200 m, 60 – 75 km westl. Shiraz, Prov. Fars, 15. – 26. 5. 1978, leg. K. ROSE“; 43: ♀, 28 mm: “Iran, Fars [sic], Kuh-e Dinar, ca. 15 km E Sisakht (Paß), 3200 m, 8. VII. 1997, leg. ECKWEILER”.

44, 45: *Zygaena* (*Agrumenia*) *naumanni* Hille & Keil, 2000; 44: Topotypus, ♂, 25 mm: “Iran, Esfahan, 20 km NW Damaneh, Kuh-Derre Bid, Godar Chonsar, 2660 m,14.6.2000, leg. KEIL“; 45: Paratypus, ♀, 27 mm: „“Iran, Esfahan, 20 km NW Damaneh, Kuh-Derre Bid, Godar Chonsar, 2660 m,7.6.99, leg. HILLE & KEIL“, ex coll. C. M. NAUMANN.

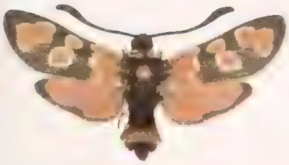
46-48: *Zygaena* (*Zygaena*) *viciae pelopis* n. subsp.; 46: Holotypus, ♂, 30 mm: „Hellas/Peloponnes, Aroania-Oros, Chelmos, Kalavrita, 1600 m, 5.-21. VII. 1987, H. ARHEILGER [leg.]“; 47: Paratypus, ♂, 31 mm: „Griechenland/Peloponnes, Prov. Achaia, Kalavrita, Aroania Oros, Mt. Chelmos, 5.-21.7.1987, 1750 m, HORST ARHEILGER leg.”; 48: Paratypus, ♂, 32 mm: „Umg. Kalaryta, 1300 m, Greece, Prov. Achaia, Peloponnes, 15.-22.6.1982, leg. T. ARHEILGER“.

49: *Zygaena* (*Zygaena*) *filipendulae noacki* Reiss, 1962; 32 mm: „Kalavrita, Prov. Achaia, Peloponnes, Griechenland, 28.5.1981, 800 m, H. ARHEILGER leg. Oberursel i. T.“.

50, 51: *Zygaena* (*Zygaena*) *viciae bosniensis* Reiss, 1922; 50: Cotype, ♂, 28 mm: „24/6 Bosnia 04, Korična, G. LEONHARD [leg.]“, ex coll. G. REISS; 51: ♂, 31 mm: „Griechenland, Thessalien, Halbinsel Pilion, Chania vic., 800 m, 26.6.1987, H. & A. HOFMANN leg.“

52-54: *Zygaena* (*Zygaena*) *filipendulae wiegelorum* n. subsp.; 52: Holotypus, ♀, 32 mm: „Turkey: Erzurum, Aşkale (7 km SW), 20. vii. 1999, W. G. TREMEWAN [leg.]“, coll. W. G. TREMEWAN; 53: Paratypus, ♂, 34 mm: „Türkei, Erzurum, 20 km nördl. Askale, Kop Gec., 1700 m, 19.7. 1992, G. BAISCH [leg.]“; 54: Paratypus, ♂, 31 mm: „Türkei, n. Askale, Kopdag, 2000 m, Tasagil, Weideland/Mähwiesen, 7.7. 1997, J.U. MEINEKE [leg.]“.

(**Fig. 52:** Holotypus, ♂, *Zygaena* (*Zygaena*) *filipendulae wiegelorum* n. subsp. in coll. W. G. TREMEWAN; alle anderen abgebildeten Tiere befinden sich in coll. A. HOFMANN/Breisach-Hochstetten; die Holotypen coll. A. HOFMANN werden später im Staatlichen Museum für Naturkunde/Karlsruhe deponiert werden).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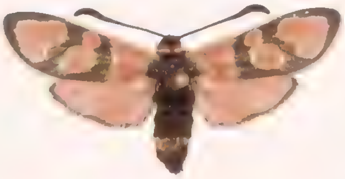
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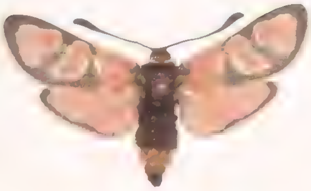
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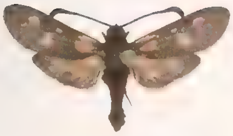
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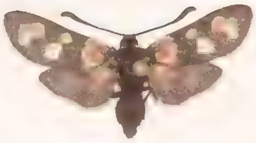
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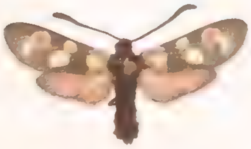
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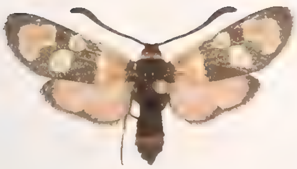
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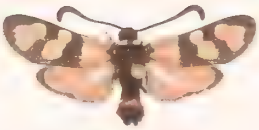
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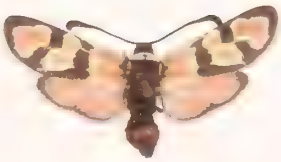
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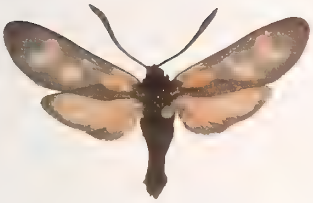
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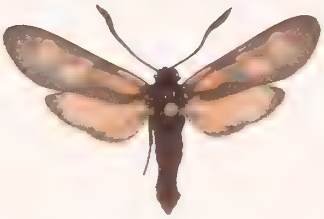
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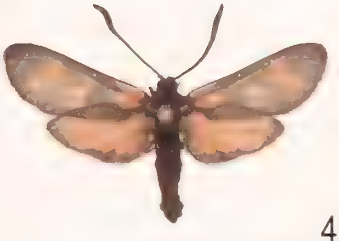
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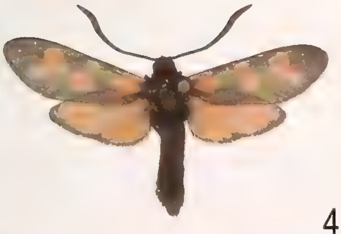
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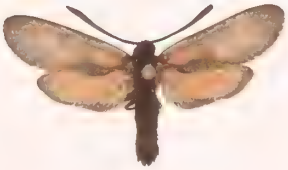
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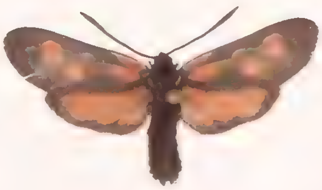
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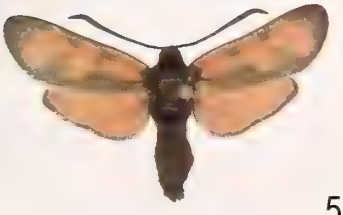
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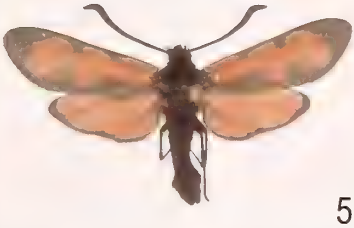
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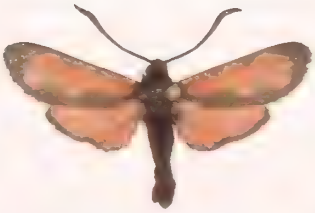
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55-57: *Zygaena* (*Zygaena*) *lonicerae pseudangelicae* n. subsp.; 55: Holotypus, ♂, 29 mm: „Türkei or., Prov. Van, Kuzgunkiran Gecidi, 1900 m, 19. –23. 7. 1981, GROß, HERBST, R. & A. HFM. [leg.]“; 56: Paratypus, ♂, 29 mm: „Türkei or., Prov. Van, Kuzgunkiran Gecidi E, Karayollari vic., 1900 – 2000 m, 14. 7. 1982, STRAUß & A. HOFMANN leg.“; 57: Paratypus, ♀, 32 mm: „Anatolien, Prov. Mus, Buğlan gecidi, 28.6. – 4.7. 1977, leg. HOLZSCHUH & RESSL“.

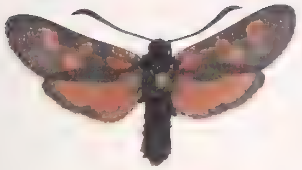
58-60: *Zygaena* (*Zygaena*) *lonicerae abbastumana* Reiss, 1922; 58: ♂, 35 mm: “Türkei sept. or., Prov. Kars, Posof 2 – 5 km E, 1750 m, 24.7. 1981, GROß, HERBST, R. & A. HFM. [leg.]“; 59: ♂, 35 mm: ibidem; 60: ♀, 37 mm: ibidem.

61: Lebensraum von *Zygaena* (*Agrumenia*) *formosa molleti* n. subsp. im Bereich der Dornpolsterstufe am Bolkar Dag-Massif unweit Ulukisla, 2600 – 3000 m, wo die Art zusammen mit *Pyrgus bolkariensis* und *Polyommatus molleti* vorkommt.

62: Raupennahrungspflanze (vermutl. *Onobrychis* spec.) von *Zygaena* (*Agrumenia*) *formosa molleti* n. subsp.

63: Eigelege von *Zygaena* (*Agrumenia*) *formosa molleti* n. subsp.

(Figs. 61–63: 4-VIII-1995, B. MOLLET phot.)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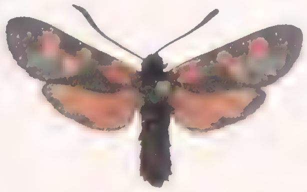
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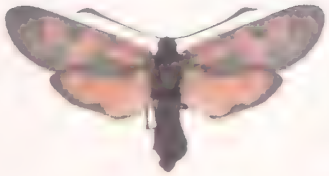
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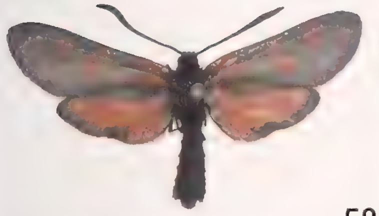
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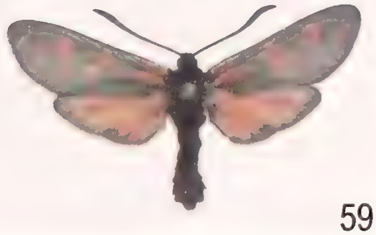
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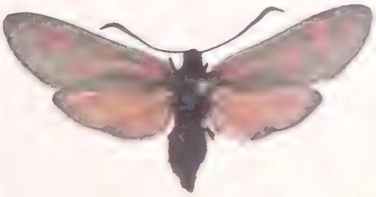
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Bonner zoologische Beiträge | Band 53 (2004) | Heft 1/2 | Seiten 99–107 | Bonn, Juni 2005

Leptopholcus (Araneae: Pholcidae) in Continental America: Rare Relicts in Low Precipitation Areas[1]

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Abstract. The genus *Leptopholcus* has a circumtropical distribution, but the only New World records previously known were for the Greater Antilles. On these islands, *Leptopholcus* is quite common, probably due to the absence of *Metagonia* from the Antilles. On the other hand, *Leptopholcus* was previously thought to be absent from the mainland where *Metagonia* is ubiquitous and species-rich, occupying the preferred habitat of *Leptopholcus* (the underside of leaves). The present paper describes three new species of *Leptopholcus* from South America: *L. brazlandia* from Distrito Federal, Brazil, *L. pataxo* from Bahia, Brazil, and *L. evaluna* from Sucre, Venezuela. All these species were collected in low numbers at low precipitation areas, and no further specimens could be found in large collections of South American pholcids, indicating a relict status of the genus in South America. The known distribution of the genus is documented, and taxonomic problems regarding its relationship with *Pholcus* and other genera are briefly discussed.

Key words. New species, taxonomy, relict, South America, competitive exclusion, *Metagonia*

1. INTRODUCTION

Representatives of *Leptopholcus* Simon, 1893 are relatively rare in collections, which is probably mainly due to their cryptic habits. Almost all known species live on the underside of leaves (PETRUNKEVITCH 1929; BRIGNOLI 1980; IRIE 1999), where they spend most of the day pressed against the surface (HUBER & PEREZ 1998). Their greenish coloration when alive and their extremely thin legs make them highly cryptic, both for predators and collectors.

SIMON (1893) created the group Leptopholceae to include pholcids with a flattened prosoma lacking depressions and sutures, and with a sternum that is longer than wide. Two genera were included: *Leptopholcus* (eight eyes) and *Micromerys* Bradley, 1877 (six eyes). Even though SIMON noted the similarities in the male genitalia between *Pholcus* Walckenaer, 1805 and *Leptopholcus*, he put *Pholcus* in a different group, the Pholceae. BRIGNOLI (1980) and DEELEMAN-REINHOLD (1986) suggested that the female external genitalia provide further means to separate *Pholcus* from *Leptopholcus*: they are covered by a chitinous plate in *Pholcus*, by unsclerotized cuticle in *Leptopholcus*. In this regard, *Leptopholcus* is similar to *Micromerys*, *Micropholcus* Deeleman-Reinhold & Prinsen, 1987 and *Calapnita* Simon, 1892. Substantial homoplasy is obviously present, and neither the relationships among genera nor the monophyly of the genera involved has ever been tested by cladistic analysis or supported by convincing arguments. Even worse, neither *Pholcus* nor *Leptopholcus* have ever been revised, and together they include some 120 nominal species. Pending a large scale revision, we consider BRIGNOLI'S (1980) statement still valid: "il conviendrait de se montrer prudent avant de réunir les deux groupes".

Considering this taxonomic situation, the assignment of the species below to *Leptopholcus* needs justification. First, we chose to follow the traditional, non-phylogenetic concept of the genus, i.e. pale pholcids with long abdomen, long and thin legs, rather flat carapace, widely spaced lateral eye triads, unsclerotized external female genitalia, and without the synapomorphies or distinctive characters of similar genera (*Panjange* Deeleman-Reinhold & Deeleman, 1983 and *Calapnita*, see DEELEMAN-REINHOLD & DEELEMAN 1986; *Micromerys*, see HUBER 2001; *Pehrforsskalia* Deeleman-Reinhold & van Harten, 2001, see DEELEMAN-REINHOLD & VAN HARTEN 2001; *Micropholcus*, see DEELEMAN-REINHOLD & PRINSEN 1987). Second, the main point of this paper is barely affected by these taxonomic problems. Neither *Pholcus* nor *Leptopholcus* (nor any of the other genera mentioned) have previously been recorded from South America [except for the synanthropic *P. phalangioides* (Fuesslin, 1775) and some taxa that were misplaced and have been transferred to New World genera; see HUBER 2000]. The only previously known autochthonous representatives of the *Pholcus*-group sensu HUBER (1995) in the New World are some *Leptopholcus* species on the Antilles and some *Pholcus* species in the eastern United States (HUBER 2000). Third, the new species seem related to the species on the Antilles (both groups have modified hairs on the tips of the male palpal trochanter apophyses), and these are presently considered as *Leptopholcus*.

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[1] In commemoration of Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004)

According to the concept above, *Leptopholcus* has a circumtropical distribution, with all known records between 29°S and 26°N. Figure 1 shows all published records (circles) as well as unpublished records (squares) of material deposited in various institutions.

DEELEMAN-REINHOLD & VAN HARTEN (2001) suggested that *Leptopholcus dioscoridis* Deeleman-Reinhold & van Harten, 2001 on Socotra Island might represent a relict. Pholcids in general, and *Leptopholcus* in particular (PETRUNKEVITCH 1929; MILLOT 1946), seem to prefer humid habitats, but Socotra has a mean annual precipitation of no more than about 170-190 mm (DEELEMAN & VAN HARTEN 2001). The three species described below might also be relicts for two reasons: first, all were collected in low precipitation areas: *L. evaluna* along a river in an area of xeric shrublands near the northern coast of Venezuela, *L. brazlandia* in 'cerrado' (i.e., tropical grasslands, savannas and shrublands), and *L. pataxo* in a transitional zone between 'cerrado' and mixed palm-sand vegetation. Second, the preferred microhabitat of *Leptopholcus* (underside of leaves) is in the New World occupied by the very species-rich genus *Metagonia* Simon, 1893. Intriguingly, *Metagonia* is absent from the Antilles (except one cavernicole species: PÉREZ & HUBER 1999), and it is only on the Antilles that *Leptopholcus* is fairly common and species-rich (HUBER 2000; see also Fig. 1).

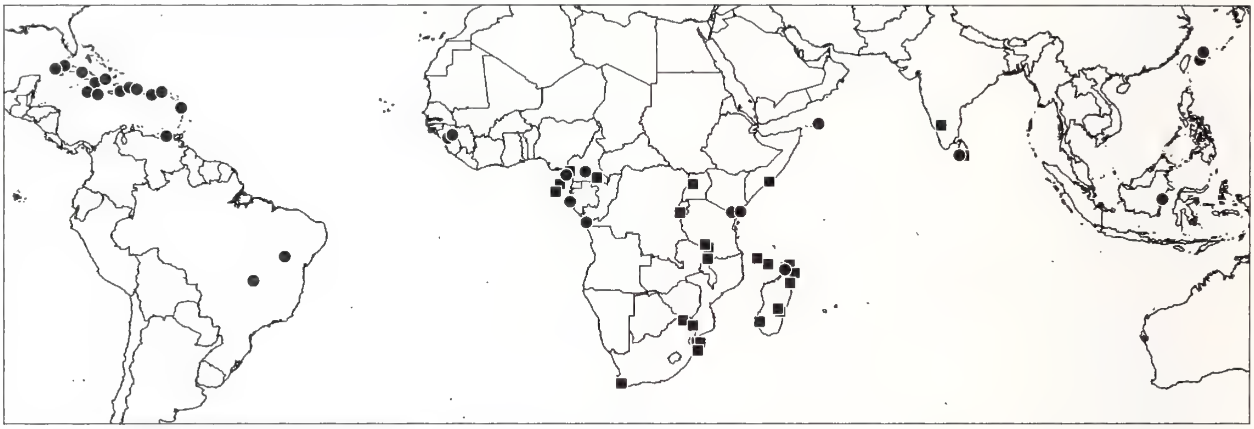


Fig. 1: Known distribution of *Leptopholcus*. Circles represent published records, squares represent unpublished material from the following institutions: National Museum of Natural History, Washington, D.C.; Zoological Research Institute and Museum Alexander Koenig, Bonn; collection Suresh Benjamin; National Museum, Bloemfontein; National Collection, Pretoria; California Academy of Sciences, San Francisco; Musée royal de l'Afrique Centrale, Tervuren.

2. TAXONOMY

Style of descriptions is as in HUBER (2000). Measurements are in mm unless indicated otherwise. Material is deposited in the Museu Nacional, Rio de Janeiro (MNRJ) and in the Museo de Historia Natural de la Fundación La Salle, Caracas (MFLS).

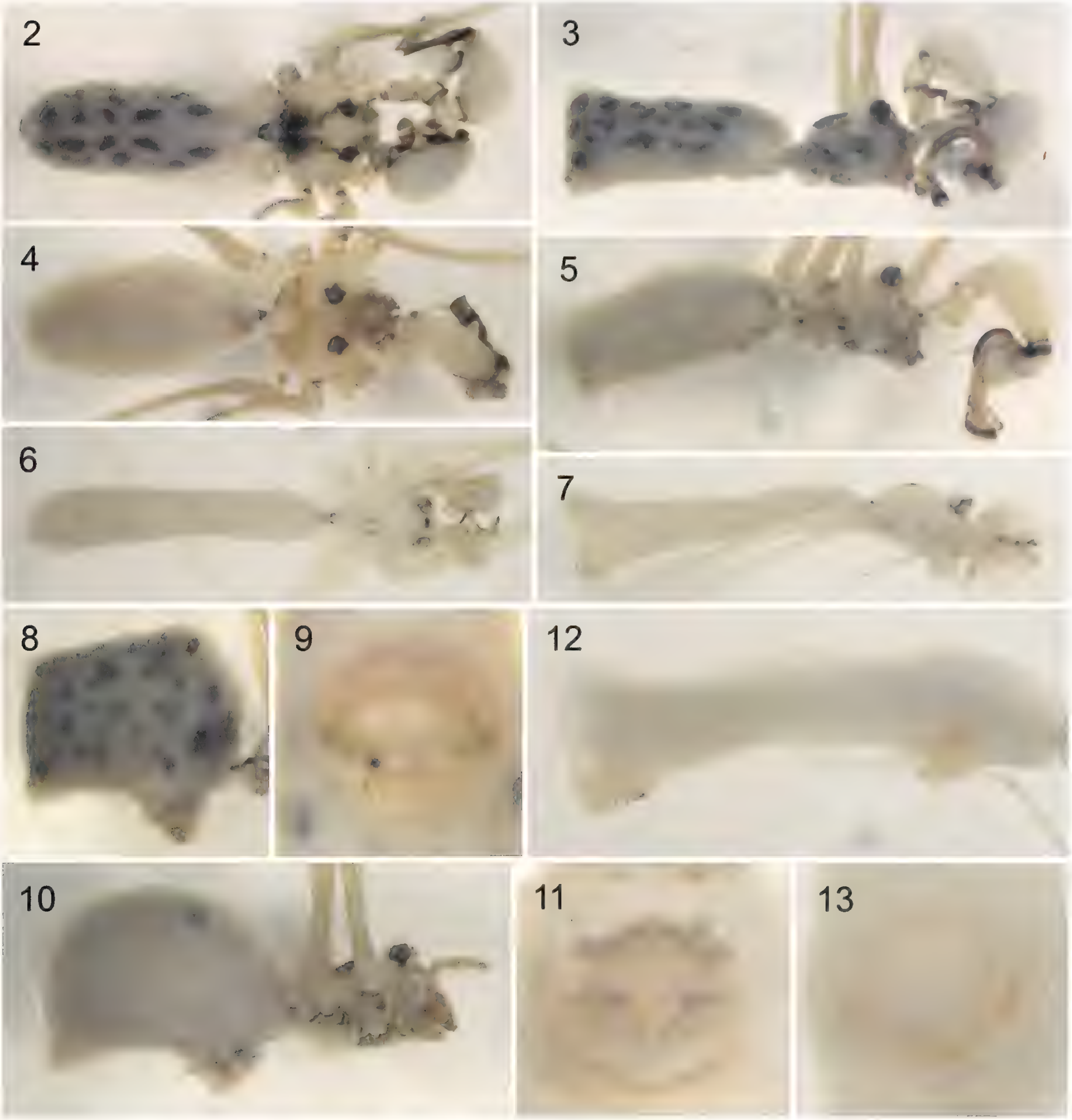
2.1. *Leptopholcus brazlandia* Huber, Pérez & Baptista, new species (Figures 2, 3, 8, 9, 14-18)

Types. Male holotype and two female paratypes from Brazlândia (15°41'S, 48°12'W), Nucleo Rural, Chacara 33, Distrito Federal, Brazil; Dec. 19, 2003 (A. Chagas, B. Segal), in MNRJ (04149-50).

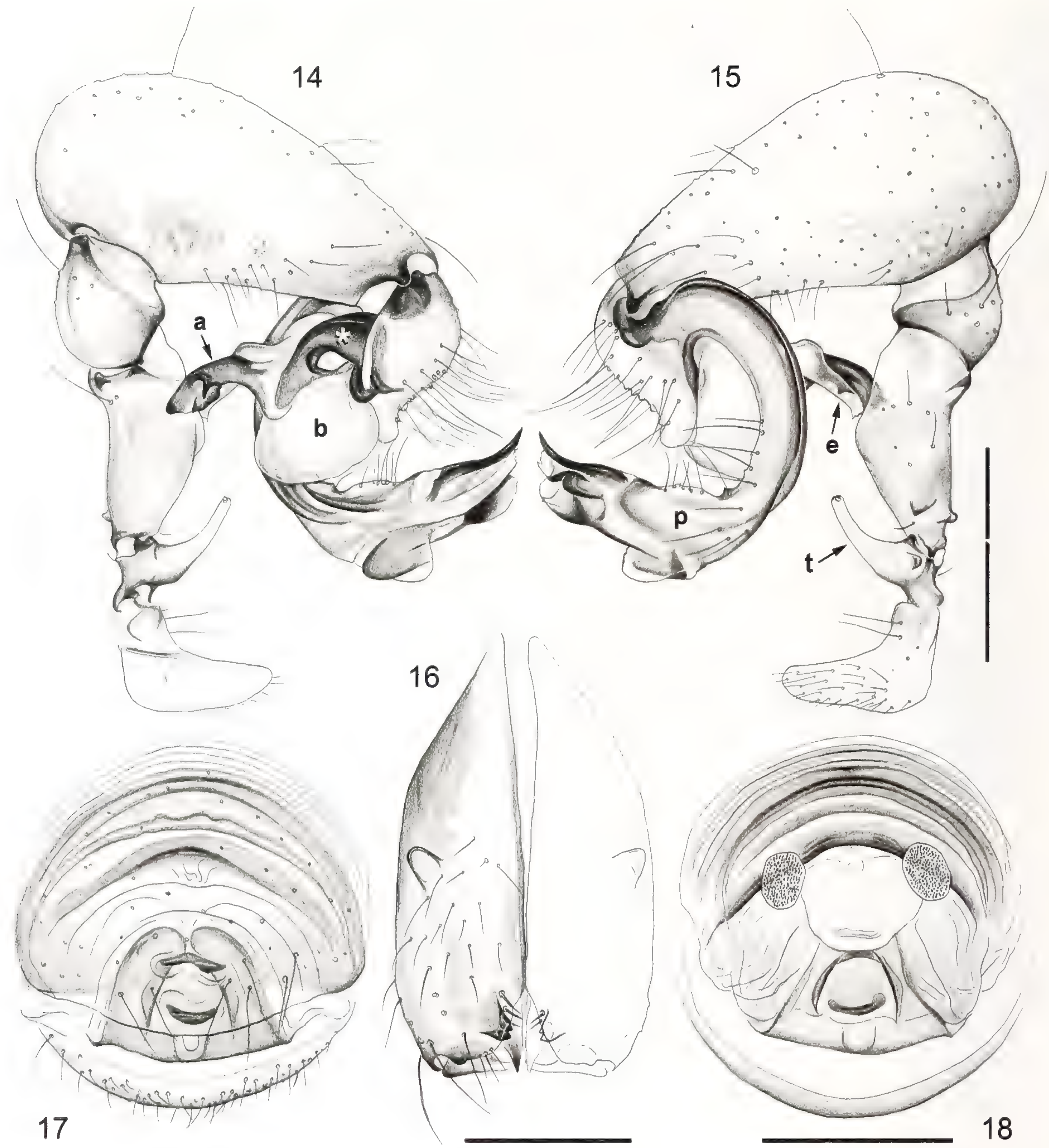
Etymology. The species name is a noun in apposition, taken from the type locality.

Diagnosis. Easily distinguished from other New World species by the spotted abdomen (Figs. 2, 3); also by the shapes of procursus, bulbal apophyses, and the internal female genital sclerites (Figs. 14, 15, 17, 18).

Male (holotype). Total length 2.8 (3.0 with clypeus), carapace width 0.97. Leg 1 missing, tibia 2: 3.8, tibia 3: 2.3, tibia 4 missing. Habitus as in Figures 2 and 3. Prosoma ochre-grey with blackish mark dorsally, clypeus barely darkened, posterior half of sternum darker, with light spots near coxae 3 and 4; legs ochre-yellow, patellae and tibia-metatarsus joints blackish; abdomen ochre-grey with many dark marks except ventrally. Ocular area slightly elevated (Fig. 3), apparently with brush of hairs between triads (most hairs missing), thoracic furrow absent; distance PME-PME 285 µm; diameter PME 90 µm; distance PME-ALE 20 µm; AME totally absent. Clypeus unmodified. Sternum wider than long (0.6/0.5), unmodified. Chelicerae as in Fig. 16, with distal apophyses carrying two modified hairs each, with some macrosetae on each side near the apophyses, proximally with slightly sclerotized projections. Palps as in Figures 14 and 15; coxa unmodified, trochanter with unsclerotized retrolateral hump and long retrolatero-ventral apophysis with modified hair distally (small and cone-shaped rather than cylindrical as in fig. 105 in Huber



Figs. 2-13: Habitus and female external genitalia photographs. 2-3. *L. brazlandia*. 4-5. *L. pataxo*. 6-7. *L. evaluna*. 8-9. *L. brazlandia*, female abdomen, lateral view, and external genitalia, ventral view. 10-11. *L. pataxo*, female, lateral view, and external genitalia, ventral view. 12-13. *L. evaluna*, female abdomen, lateral view, and external genitalia, ventral view.



Figs. 14-18: *L. brazlandia*, left male palp in prolateral (14) and retrolateral (15) views, male chelicerae (16), and cleared female genitalia in ventral (17) and dorsal (18) views. **a:** appendix, **b:** bulb, **e:** embolus, **p:** procursus, **t:** trochanter-apophysis, asterisk: proximal sclerotized element of bulb. Scale lines: 0.5 mm (14, 15), 0.2 mm (16), 0.3 mm (17, 18).

2000); femur with indistinct ventral protrusion and two distinct retrolateral apophyses; procursus relatively simple except distally, with capsulate tarsal organ; bulb with proximal sclerotized element, apparently without uncus, with complex appendix(?) and slightly sclerotized embolus. Retrolateral trichobothrium of tibia 2 at 15%; legs apparently without spines, curved hairs, and vertical hairs (most hairs missing); tarsus 2 with about 10 fairly distinct pseudosegments. Abdomen posteriorly pointed dorsally (Fig. 3).

Female (paratype). In general similar to male. Tibia 1 missing in both specimens. Female external genitalia protruding but simple (Figs. 8, 9), consisting of frontal plate and smaller median plate that carries a small indistinct knob-like structure. Internal genitalia with complex system of distinctive sclerites and folds (Figs. 17, 18).

Distribution. Known only from type locality.

Remarks. The collecting area is located near the borders of the Cupim river, at the northeast of the Federal District. The Cupim river flows down the Chapada da Contagem flanks, forming a series of rapids known locally as Mumunhas. The specimens were collected in gallery forest at the borders of one of the rapids. That spot is much more humid than the xeric 'cerrado' areas around it. The type locality is part of an area preserved by Brazilian Government, the Área de Proteção Ambiental de Cafuringa.

2.2. *Leptopholcus pataxo* Huber, Pérez & Baptista, new species (Figures 4-5, 10-11, 19-23)

Types. Male holotype, seven female paratypes and 2 juveniles from Gentio do Ouro, Toca do Encantado (11°25'S, 42°30'W), Bahia, Brazil; Nov. 10, 2002 (R.L.C. Baptista, A.P.L. Giupponi), in MNRJ (04147-48).

Etymology. The species name honours the Pataxó-Hãhãhãi Indians, formerly one of the largest Indian tribes in Bahia state. Only a few isolated communities remain, mainly due to extermination campaigns to clear land for cacao plantations. The epithet is a noun in apposition.

Diagnosis. Distinguished from other New World species by the shapes of procursus, bulbal apophyses, and the internal female genital sclerites (Figs. 19, 20, 22, 23).

Male (holotype). Total length 3.2 (3.4 with clypeus), carapace width 1.13. Leg 1: 8.7 + 0.5 + 8.3 + 15.3 (tarsus missing), leg 2 missing, tibia 3: 2.9, tibia 4: 4.1; tibia 1 L/d: 85. Habitus as in Figures 4 and 5. Prosoma pale ochre-grey with pair of brown marks dorsally and brown mark on clypeus, sternum light brown except frontally; legs ochre-yellow, patellae and tibia-metatarsus joints brown; abdomen monochromous ochre-grey, ventrally with pair of brown marks in booklung-area. Ocular area slightly elevated (Fig. 5), with brush of hairs between triads, thoracic furrow absent; distance PME-PME 375 µm; diameter PME 105 µm; distance PME-ALE 25 µm; AME-AME 15 µm, AME diameter 20 µm. Clypeus unmodified. Sternum wider than long (0.75/0.55), unmodified. Chelicerae as in Fig. 21, with distal apophyses carrying four modified hairs each, with some macrosetae on each side near the apophyses, proximally with slightly sclerotized projections. Palps as in Figures 19 and 20; coxa unmodified, trochanter with unsclerotized retrolateral hump and long retrolatero-ventral apophysis with characteristic modified hair distally (cf. fig. 105 in Huber 2000); femur with large ventral protrusion and two distinct retrolateral apophyses; procursus relatively simple except distally, with capsulate tarsal organ; bulb with proximal sclerotized element connected to small uncus(?), with complex appendix and slightly sclerotized long embolus (Fig. 19). Retrolateral trichobothrium of tibia 1 at 7%; tibia 1 without prolateral trichobothrium (present in all others); legs without spines, curved hairs, and vertical hairs; tarsus 3 with about 7 fairly distinct pseudosegments. Abdomen posteriorly not pointed dorsally (Fig. 5).

Female (paratype). In general similar to male, but abdomen thicker, clypeus barely darker. Tibia 1 in 4 females: 5.5-6.8. External genitalia protruding but very simple externally (Figs. 10, 11), apparently without knob-like structure. Internal genitalia with complex system of distinctive sclerites and folds (Figs. 22, 23).

Distribution. Known only from type locality.

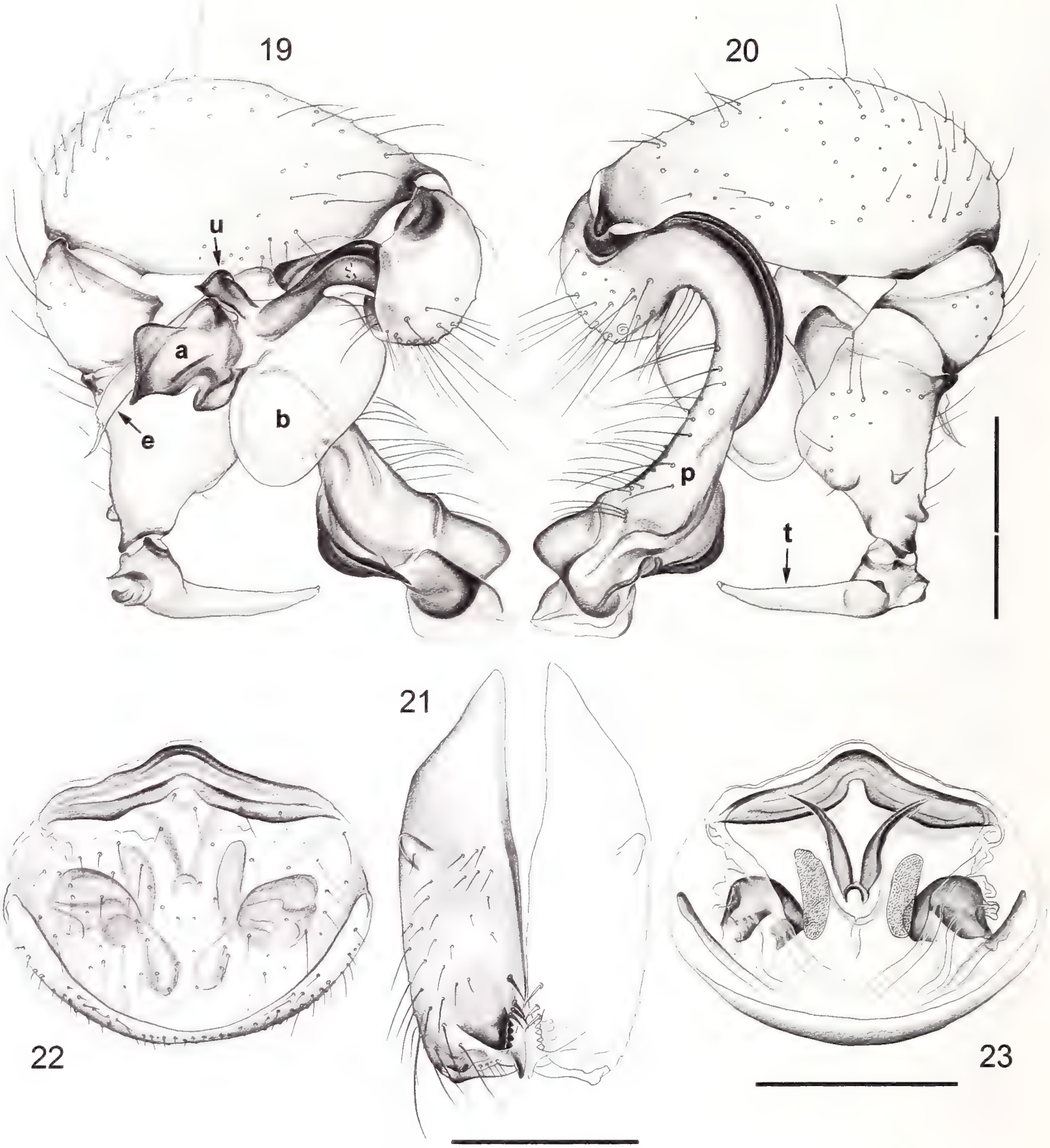
Remarks: The collecting area is located at the border of a small stream, the Encantado river, at less than 15 km from the São Francisco river. It is a small rocky gorge with the stream flowing through it and forming isolated ponds. Most of the area between the São Francisco river and Toca do Encantado is covered by a mixed vegetation of palms, trees and shrubs over a sandy and damp soil. The higher areas after Toca do Encantado are covered by a transitional xeric vegetation of 'cerrado'-'caatinga', over a rocky soil. All the *Leptopholcus* specimens were collected from webs placed against the underside of big boulders at the stream borders. The spiders were closely pressed against the rock, in a manner similar to other species of *Leptopholcus* that live on the underside of leaves. A search for *Leptopholcus* on the underside of leaves was made in the area, but no specimen was found. However, only a few bushes, palms and trees with small leaves cover the stream borders, which would not offer an adequate substrate for *Leptopholcus*.

2.3. *Leptopholcus evaluna* Huber, Pérez & Baptista, new species (Figures 6-7, 12-13, 24-28)

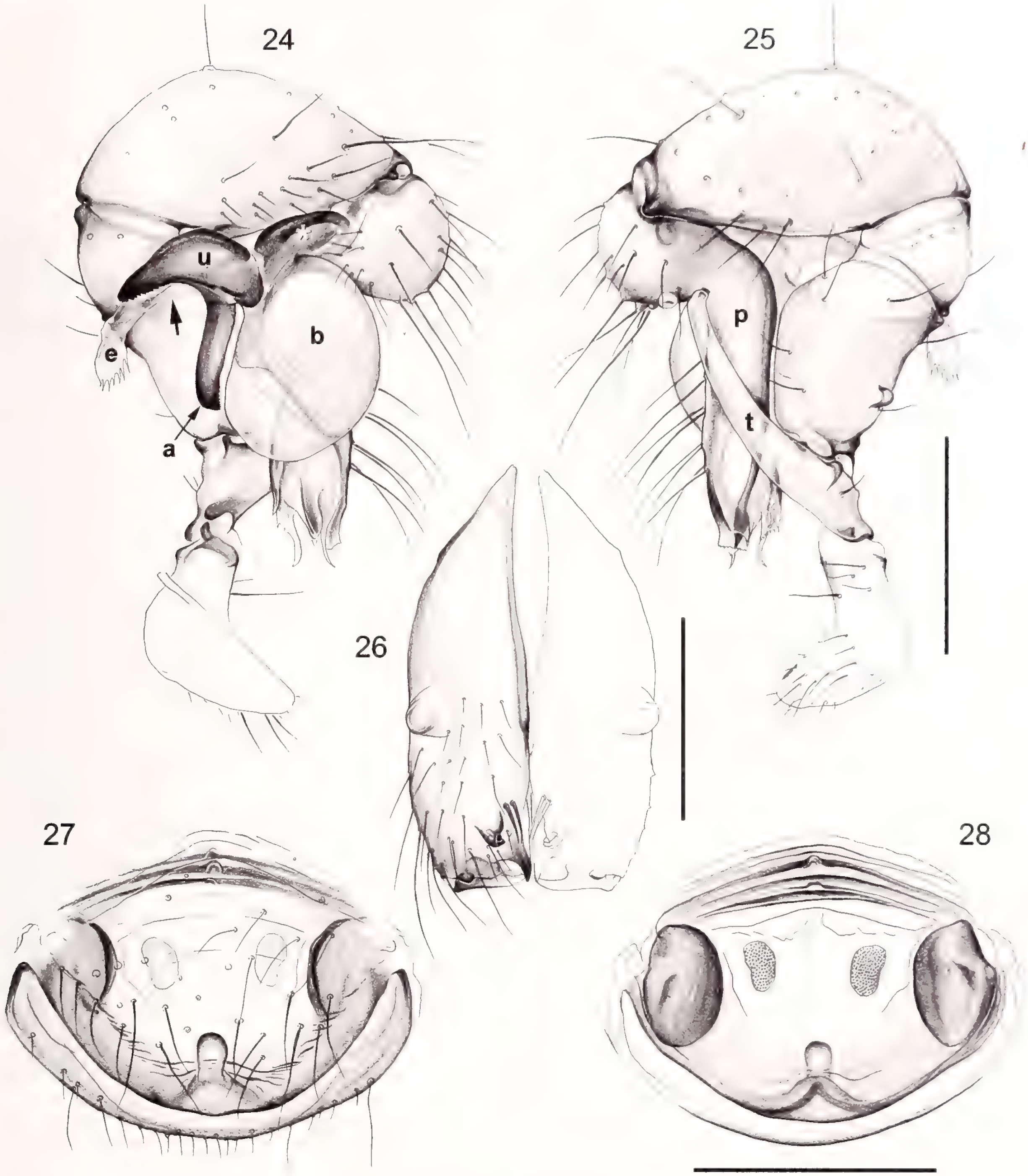
Types. Male holotype and one female paratype from underside of leaves along riverbed, Marigüitar (10°26.5'N, 63°54.5'W), ~30 m a.s.l., Sucre, Venezuela; Nov. 29, 2002 (B. A. Huber), in MFLS.

Etymology. Named for Isabel Allende's Venezuela-born protagonist and fantastic story-teller. The epithet is a noun in apposition.

Diagnosis. Distinguished from other New World species by the very long male palpal trochanter apophysis, and by the shapes of procursus, bulbal apophyses, and internal female genital sclerites (Figs. 24, 25, 27, 28).



Figs. 19-23: *L. pataxo*, left male palp in prolateral (19) and retrolateral (20) views, male chelicerae (21), and cleared female genitalia in ventral (22) and dorsal (23) views. **a:** appendix, **b:** bulb, **e:** embolus, **p:** procursus, **t:** trochanter-apophysis, **u:** uncus, asterisk: proximal sclerotized element of bulb. Scale lines: 0.5 mm (19, 20, 22, 23), 0.3 mm (21).



Figs. 24-28: *L. evaluna*, left male palp in prolateral (24) and retrolateral (25) views, male chelicerae (26), and cleared female genitalia in ventral (27) and dorsal (28) views. **a:** appendix, **b:** bulb, **e:** embolus, **p:** procursus, **t:** trochanter-apophysis, **u:** uncus, asterisk: proximal sclerotized element of bulb, arrow points to transparent projection of bulb. Scale lines: 0.3 mm (24, 25, 27, 28), 0.2 mm (26).

Male (holotype). Total length 2.95 (3.05 with clypeus), carapace width 0.77. Leg 1: 26.8 (6.5 + 0.4 + 6.4 + 12.4 + 1.1), tibia 2: 4.1, tibia 3: 2.5, tibia 4: 3.6; tibia 1 L/d: 96. Habitus as in Figures 6 and 7. Entire animal very pale whitish (in live rather greenish), with pair of dark dots on carapace, patellae and tibia-metatarsus joints slightly darkened, abdomen dorsally with two pairs of indistinct dark marks. Ocular area barely elevated (Fig. 7), only triads on low elevations, thoracic furrow absent; distance PME-PME 195 µm; diameter PME 70 µm; distance PME-ALE 20 µm; AME-AME 20 µm, AME diameter 30 µm. Clypeus unmodified. Sternum wider than long (0.55/0.45), unmodified. Chelicerae as in Fig. 26, with distal apophyses carrying two (or three?) modified hairs each, with two macrosetae on each side near the apophyses, proximally with unsclerotized projections. Palps as in Figures 24 and 25; coxa unmodified, trochanter with short retrolateral apophysis and very long retrolatero-ventral apophysis with characteristic modified hair distally (cf. fig. 105 in Huber 2000), femur with distinct retrolateral apophysis, procursus relatively simple, with capsulate tarsal organ, distally more complex with various membranous structures, bulb with proximal sclerotized element, sclerotized uncus and appendix and membranous embolus with distal transparent fringes, with additional slender transparent projection (arrow in Fig. 24). Retrolateral trichobothrium of tibia 1 at 8%; tibia 1 without prolateral trichobothrium (present on other legs); legs without spines, curved hairs, and vertical hairs; tarsus 1 apparently with >20 pseudosegments, but very indistinct and difficult to see, only distally about 5 fairly distinct. Abdomen posteriorly slightly pointed dorsally (Fig. 7).

Female. In general similar to male, but without dark spots on carapace. Tibia 1: 5.1. External genitalia very simple, slightly protruding (Figs. 12, 13), with distinct knob at posterior rim (Fig. 27), with small oval pore plates (Fig. 28).

Distribution. Known only from type locality.

Acknowledgements. We thank Osvaldo Villarreal, Celsa Señaris and Daniel Lew for their support in obtaining a collecting permit in Venezuela and for the loan of specimens, the Dirección General de Fauna y Oficina Nacional de Diversidad Biológica in Caracas for issuing permit N° 01-11-0966, and the Deutsche Forschungsgemeinschaft for financing a collecting trip to Venezuela (DFG grant HU 980/1-1). Venezuelan results are part of the project "Expedición Aracnológica a Venezuela", between the Zoological Research Institute and Museum Alexander Koenig, the arachnological laboratory of the National Museum of the Federal University of Rio the Janeiro and the Natural History Museum of the "La Salle" Foundation, Caracas. Thanks are also due to Pedro Gnaspini and FAPESP for funding the "Expedição Amblypygi" to Bahia State, Brazil, to Alessandro Giupponi, Amazonas Chagas Jr. and Barbara Segal for collecting specimens, to Frederico Araujo Ramos for providing information about the type locality of *L. brazlandia* and to Adriano B. Kury for the loan of the Brazilian specimens.

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Bonner zoologische Beiträge	Band 53 (2004)	Heft 1/2	Seiten 109–110	Bonn, Juni 2005

First Record of *Hyles dahlii* (Geyer, 1827) (Lepidoptera: Sphingidae) from the African Mainland[1]

Anna K. HUNDSDÖRFER, Dresden

The hawkmoth species *Hyles dahlii* (Geyer, 1827) is considered to be restricted to Corsica, Sardinia and the Balearic Islands (REBEL 1934), although there are occasional reports from Sicily (PITTAWAY 2004). In addition, it has also been found on the Catalan coast, in northeastern Spain, in 1975 (MASÓ PLANAS et al. 1979) and on the island of Pianosa, off the Tuscan coast (Italy) in 1998 (DAPPORTO et al. 1999).

Here I report the discovery of about 15-20 first instar (L1) larvae of *H. dahlii* feeding on *Euphorbia paralias* in northern Tunisia in October 2004. The exact locality is the beach at Residence Shiri, a small hotel and camping site on the coast north of Sejane between Cap Serrat and Bizerte. I collected and reared about a dozen individuals. After two moults it was possible to determine them as *H. dahlii* (a caterpillar is illustrated in Fig. 1 and an adult in Fig. 2). This species has to date not been reported from Africa. Voucher specimens will be deposited at the Zoologisches Forschungsinstitut und Museum Alexander Koenig (Bonn) and the Natural History Museum (London).

I doubt that *H. dahlii* is already established on the African mainland. I observed very few habitats for spurge-feeding hawkmoths in Tunisia, as I found little food plant in the parts of the country I visited. During my one-week tour (from the northern coast due south near the Algerian border, then back north along the eastern coast), I found herbaceous *Euphorbia* only along one inland stretch of road; otherwise there was only *E. paralias* along the coast. In the north, there are few sandy coastlines and these are often short and very isolated, with stretches of rocky coast and cultivated pine forest surrounding them. In parts of the eastern coast, the air is so humid that water condenses on the plants and the sand becomes baked onto them, so that they do not appear to be easily eatable by caterpillars. Also, the beaches are often partly or wholly developed for the tourist industry and thus it is possible that the populations of *E. paralias* have become relictual or destroyed due to human activities. I found no other *Hyles* caterpillars at the beach of Residence Shiri, or any indications of prior occurrence, such as droppings or nibbled plant sprouts. In contrast, on other beaches in Tunisia, and one especially on the north coast, as well as at one locality inland, I found numerous caterpillars of *H. tithymali*, but I did not find any other *H. dahlii* caterpillars. Therefore, I consider this first record of *H. dahlii* from the African mainland is probably the result of a rare dispersion event, possibly of only a single fertilised female from Sardinia, which lies geographically nearest to the Tunisian locality.

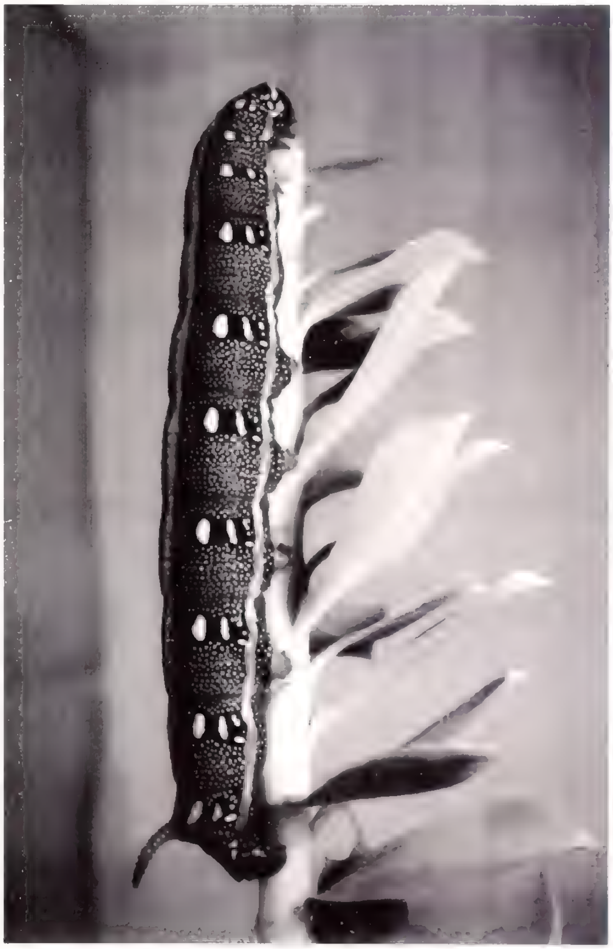

Fig. 1: Fifth instar larva of *Hyles dahlii* found on *Euphorbia paralias* in Tunisia in October 2004 (feeding in captivity on *E. myrsinites*).

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[1] Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004) zum Gedenken

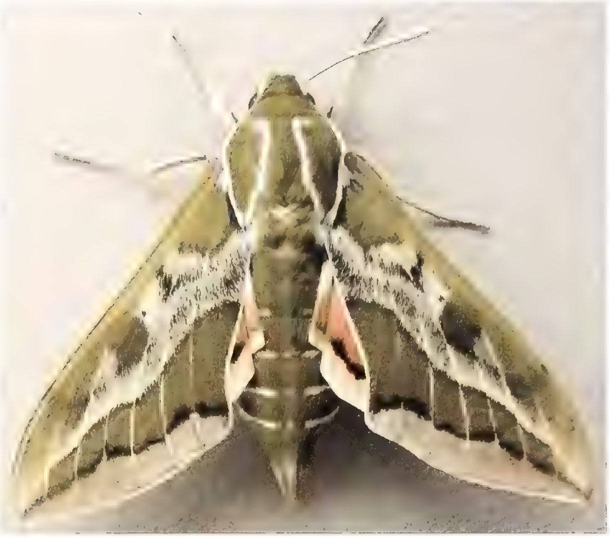

Fig. 2: An adult moth of *Hyles dahlii*, emerged from the pupa in February 2005. The individual was collected as first instar larva in Tunisia in October 2004 and reared in captivity.

Acknowledgements. I would like to thank Michael Korn (Konstanz) for this successful joint collecting trip to Tunisia and his specific help in looking out for *Euphorbia* plants and *Hyles* caterpillars. Special thanks also go to Paolo Mazzei (Rome), who first determined these larvae as *H. dahlii* on the basis of the single specimen I gave to him during my return journey. I am indebted to Ian J. Kitching (London) for his correction of my language and for very helpful suggestions to this note. I would also like to express gratitude to the late Clas Naumann for his long-term interest and participation in the collection of *Hyles* samples for our joint studies with Ian J. Kitching and Michael Wink (Heidelberg).

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Bonner zoologische Beiträge	Band 53 (2004)	Heft 1/2	Seiten 111–114	Bonn, Juni 2005

A New Genus and Species of Scorpion from Afghanistan (Scorpiones, Buthidae)[1]

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Abstract. A new genus and species of a psammophilic buthid scorpion, *Afghanobuthus naumanni* gen. n., sp. n., are described on the basis of one female specimen collected by Professor Clas Naumann on October 1971 in Afghanistan. The specimen was collected in an extremely arid zone (400 m), at Vic Shiberghan, Dasht-e-Leili on the North range of the country.

1. INTRODUCTION

In a recent publication, FET et al. (2001) call attention to the important and interesting diversity of psammophilic scorpions, from the Palaearctic deserts of central and southern Asia. In this contribution, the authors described a new genus and species of a buthid scorpion from the Baluchistan Province of Iran. They also included a very complete table of characters for six buthid psammophilic genera, namely, *Anomalobuthus* Kraepelin, 1900, *Liobuthus* Birula, 1898, *Plesiobuthus* Pocock, 1990, *Psammobuthus* Birula, 1911, *Pectinibuthus* Fet, 1984 and *Polisius* Fet, Capes & Sissom, 2001.

During his field trips to Afghanistan on the early 1970s Professor Clas Naumann collected a few scorpions, which were subsequently sent to Prof. Max Vachon in Paris. After examination, Vachon determined two specimens as *Compsobuthus* sp. A recent study of these two specimens revealed that the one collected in the eastern region of the country, S of Kunduz (Qonduz), NE of Pul-I-Khumri (Poi-e-Khomri), on April 7, 1972 was indeed a species of *Compsobuthus*. This specimen was described as a new species, *Compsobuthus tofti* Lourenço, 2001 (LOURENÇO 2001a).

Careful examination of the second specimen revealed that it was not a *Compsobuthus*, but rather a psammophilic element. From the table of characters proposed by FET et al. (2001), it appears that the specimen from Afghanistan shares some common characters with the listed genera. It shows, however, a combination of different characters, and this leads me to describe here a new genus and species. This new scorpion was collected by Professor Clas Naumann in October 1971, on the North range of the country, at Vic Shiberghan, Dasht-e-Leili.

2. TAXONOMIC TREATMENT

Afghanobuthus gen. n.

Diagnosis. Small sized scorpions, 27.3 mm in total length. Colouration of a generally pale yellow without any spots or pigmented zones on the body and its appendages. Dentate margins on movable and fixed fingers of pedipalp chela composed of 11/12 almost linear rows of granules. Absence of inner and outer denticles on both fingers. Pectinal tooth count 24-25. Chelicerae with one basal denticle on the fixed finger flattened in its apex; basal denticles of the movable finger absent. Anal arc with 3 lateral lobes. Trichobothrial pattern A-β (Beta).

Derivatio nominis: After Afghanistan, its country of origin.

Relationships: From its general morphology, the new genus *Afghanobuthus* gen. n. appears to have some relationships with other psammophilic genera present in the Palaearctic deserts, but also in North African deserts. It shares with other genera such as *Polisius*, *Anomalobuthus* or *Plesiobuthus* an orthobothriotaxy pattern for trichobothria. It also shares with *Pectinibuthus*, *Anomalobuthus* and the Somalian genus *Sabinebuthus* Lourenço, 2001 (LOURENÇO 2001b) a very slender chela with rows of granules essentially straight. The new genus can, however, be readily distinguished from other psammophilic genera, by a combination of characters: (i) Basal denticles of chelicera movable finger absent. (ii) Absence of inner and outer accessory denticles on pedipalp chela fingers. (iii) Sternum pentagonal. (iv) Small size.

Type species *Afghanobuthus naumanni* sp. n.

Description:

Afghanobuthus naumanni sp. n. (Figs. 1-8)

Diagnosis: as for the new genus.

Type material: 1 female holotype, Afghanistan, North range, Vic Shiberghan, Dasht-e-Leili, 400 m, X/1971

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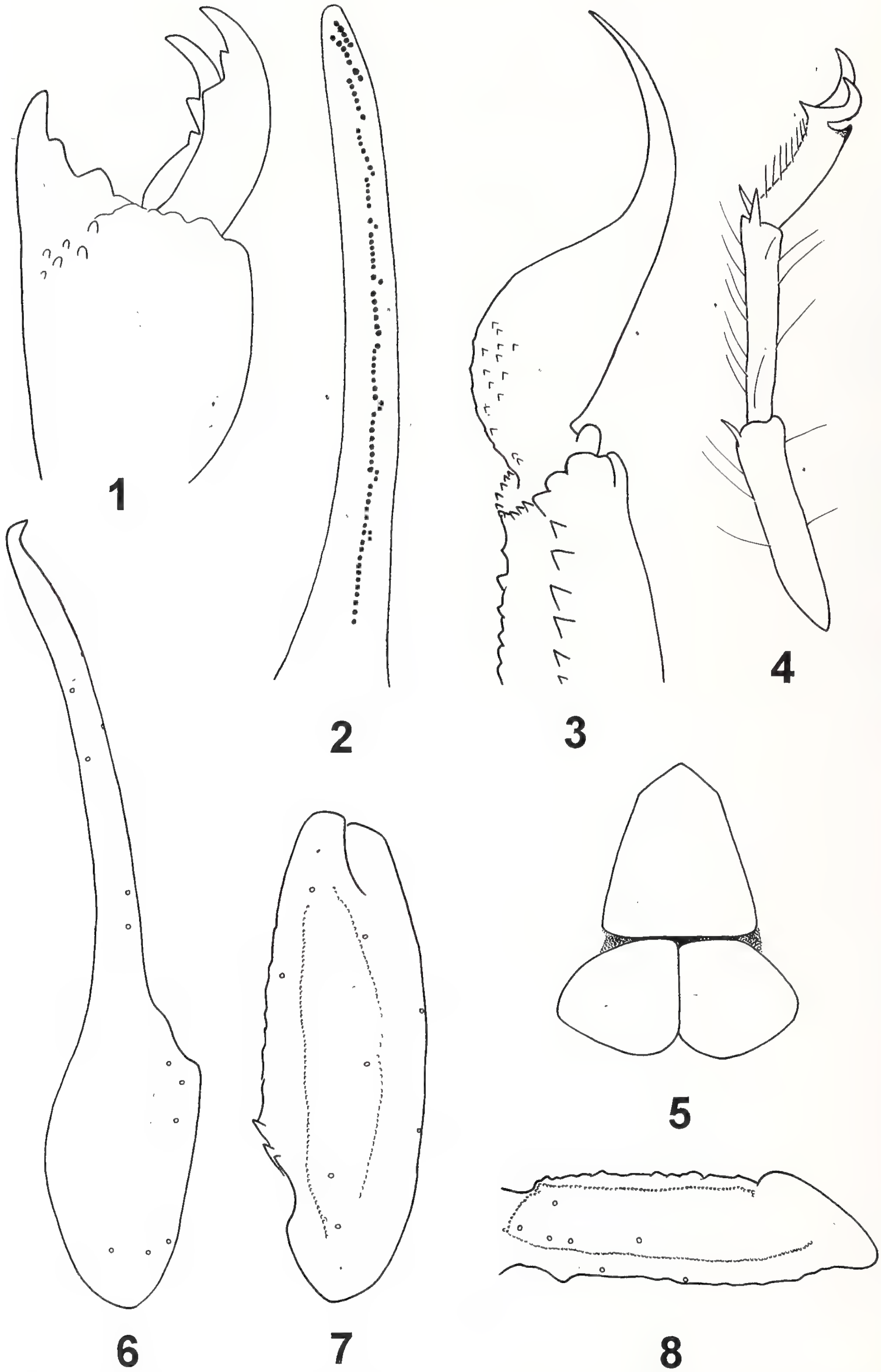
[1] In commemoration of Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004)



Figs. 1-8: *Afghanobuthus naumanni* gen. n., sp. n. Female holotype. 1. Chelicera, 2. Movable finger of pedipalp chela with almost linear rows of granules. 3. Metasomal segment V and telson, lateral aspect, showing anal arc. 4. Leg IV with tibial and pedal spurs. 5. Sternum and genital operculum. 6-7. Trichobothriotaxy. 6. Chela, dorso-external aspect. 7. Patella, dorsal aspect. 8. Femur, dorsal aspect.

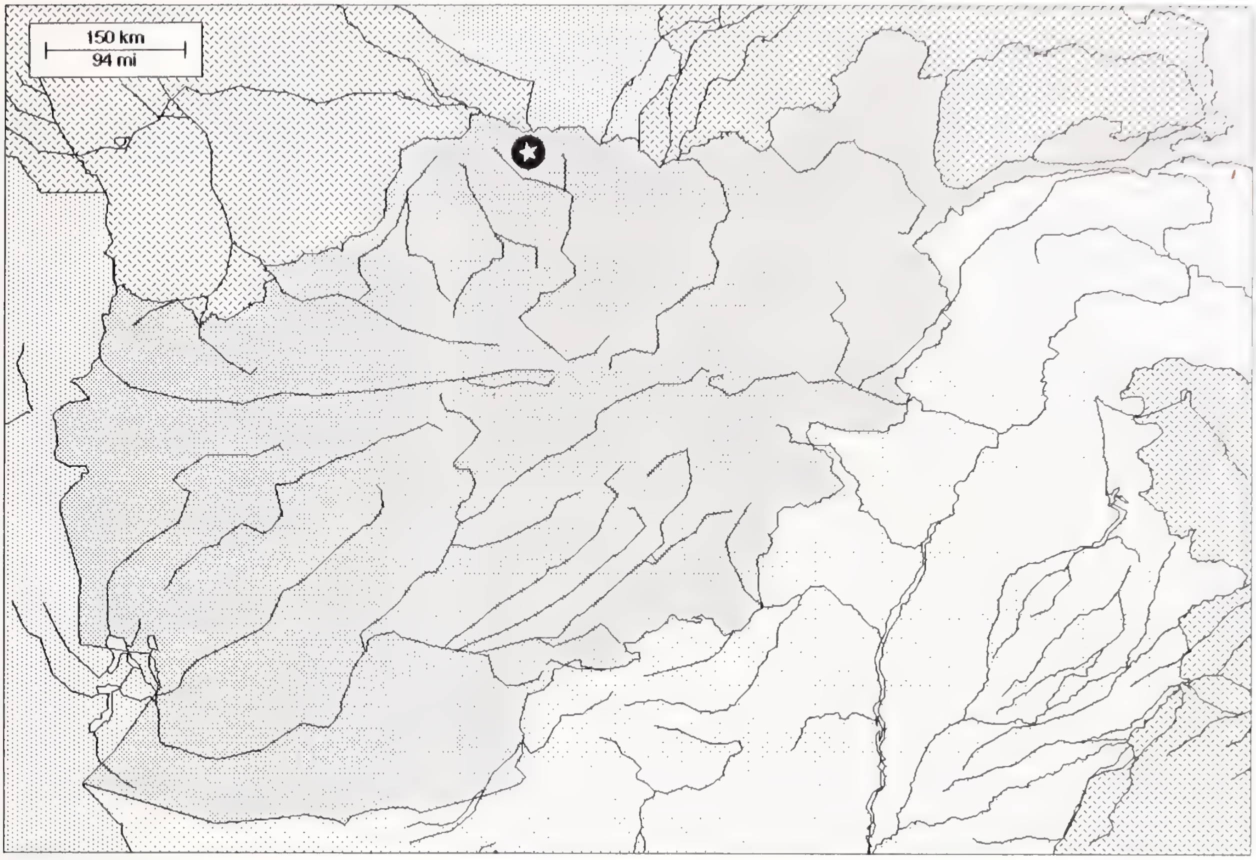


Fig. 9: Map of Afghanistan showing the type locality of the new species.

(C. Naumann leg.). Deposited in the collection of the 'Muséum national d'Histoire naturelle', Paris.

Patronym: In honour of the late Professor Clas M. Naumann, Zoologisches Forschungsinstitut und Museum Alexander Koenig (ZFMK), Bonn (Germany), who collected the specimen and contributed significantly to the scientific infrastructure of Afghanistan.

Description based on female holotype (Morphometric measurements in Table 1).

Table I: Morphometric values (in mm) of the female holotype of *Afghanobuthus naumanni* gen. n., sp. n.

Total length	27.3
Carapace:	
- length	3.5
- anterior width	2.4
- posterior width	3.7
Metasomal segment I:	
- length	2.1
- width	1.9
Metasomal segment V:	
- length	3.9
- width	1.7
- depth	1.6
Vesicle:	
- width	1.2
- depth	1.2
Pedipalp:	
- Femur length	3.1
- Femur width	0.9
- Patella length	4.1
- Patella width	1.3
- Chela length	6.4
- Chela width	1.1
- Chela depth	1.1
Movable finger:	
- length	4.6

Colouration. Generally pale yellow without any spots or pigmented zones on body and appendages. Prosoma: carapace yellowish; only eyes surrounded by black pigment. Mesosoma: yellowish. Metasoma: all segments yellowish. Vesicle yellowish; aculeus yellowish at base and light reddish at extremity. Venter pale yellow. Chelicerae yellowish; teeth light reddish. Pedipalps: yellowish overall; rows of granules on dentate margins of fingers very slightly darker. Legs yellowish.

Morphology. Prosoma: anterior margin of carapace weakly emarginate. Carapace carinae weakly to moderately developed; anterior median carinae moderate to weak; posterior median carinae moderate; central lateral moderate to weak; central median vestigial; posterior median carinae not terminating distally in spinoid process. Intercarinal spaces somewhat moderately granular laterally; almost smooth centrally. Median ocular tubercle slightly anterior to centre of carapace; median eyes separated by 2.5 ocular diameters. Three pairs of lateral eyes. Mesosoma: Tergites I-VI tricarinate. Lateral carinae on I-VI moderate to weak, granular; each carina terminating distally in very small spinoid process that extends very slightly beyond posterior margin of tergite. Median carinae on I weak; on II-VI moderate, to weak, terminating slightly distally on each segment with spinoid process that extends very slightly beyond posterior margin of tergite. Tergite VII pentacarinate, with lateral pairs of carinae moderate to strong; median carinae present on proximal half, moderate. Intercarinal spaces weakly granular, almost smooth. Sternites: absent from sternites III-VI; Sternite VII with 4 carinae moderate to weak. Pectines moderately long; pectinal tooth count 24-25. Metasoma: Segments I-II with 10 carinae, crenulate; III-IV with 8 carinae. Dorsolateral carinae moderate, without spinoid denticles. Ventral submedian carinae moderate on segments I-IV. Segment V with 5 carinae; ventromedian carinae moderate to strong. Dorsal furrows of all segments moderately to weakly developed, smooth; intercarinal weakly granular almost smooth. Telson weakly granular, almost smooth, with only some granules ventrally; aculeus weakly curved, and slightly longer than vesicle. Subaculear tubercle absent. Chelicerae: Basal denticles of movable finger absent; basal denticles of fixed finger flattened at apex (Vachon, 1963). Pedipalps: Trichobothrial pattern orthobothriotaxic, type A (Vachon, 1974); dorsal trichobothria of femur in β (beta) configuration (Vachon, 1975). Femur pentacarinate; all carinae moderately crenulate. Patella with 8 carinae; all carinae weak; dorsointernal carinae with one slightly spinoid granule. Chelae slender, with elongated fingers; all carinae weak to vestigial. Dentate margins on movable and fixed fingers composed of 11/12 almost linear rows of granules. Legs: Ventral aspect of tarsi with one row of thin setae. Tibial spurs present on legs III-IV but reduced; pedal spurs present on all legs, moderate to strong.

Acknowledgements. I am very grateful to J. Köhler (ZFMK, Bonn) for inviting me to participate in this publication and to B. Sinclair (ZFMK, Bonn) for reviewing the English style of preliminary drafts of the manuscript.

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Bonner zoologische Beiträge | Band 53 (2004) | Heft 1/2 | Seiten 115–119 | Bonn, Juni 2005

Two New Species of *Eoophyla* Swinhoe, 1900 from Continental South East Asia (Lepidoptera: Crambidae, Acentropinae)[1]

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Abstract. *Eoophyla clasnaumanni* Speidel & Mey sp. nov. from North Thailand and *Eoophyla myanmarica* Mey & Speidel sp. nov. from North-west Myanmar (Burma) are described. These new species are closely related to each other and to *Eoophyla aureolalis* (Snellen, 1876) from Sundaland. Differential characters and figures of all three species are provided.

1. INTRODUCTION

The species of *Eoophyla* Swinhoe, 1900 are currently placed in a number of species groups. SPEIDEL & MEY (1999) recognised six groups including an assemblage of nine isolated species which could not be assigned then to one of the defined groups. The study of the Philippine species of the genus resulted in the establishment of three further groups (SPEIDEL 2003). The definition of the groups are based on external characters. Especially the number and arrangement of the eye-spots on the hindwings are used as a simple and discernable trait. It has proved to be a practical way in sorting species and to cope with the increasing species numbers. The species treated in this paper belong to the *crassicornalis* group of species (SPEIDEL & MEY 1999). Since the phylogenetic value of this and other characters is unclear yet, the ordering group system of the genus should be regarded as provisional.

The Acentropinae collection in the ZMHB and the collection of W. Speidel contain a number of undescribed species. In the *crassicornalis* – group *Eoophyla aureolalis* (Snellen, 1876) is the only species hitherto known with a dark spot in the anal field of the forewings. The species is distributed in Sundaland. The examination of specimens with the same wing pattern from Thailand and Myanmar showed that they are related to *E. aureolalis* but represent separate species. They are described in the present paper.

Abbreviation: ZMHB = Museum für Naturkunde, Humboldt Universität, Berlin

2. DESCRIPTION OF SPECIES

Eoophyla clasnaumanni Speidel & Mey, sp. nov.

Material: Female holotype (genitalia slide: Mey 10/04) and 1 male paratype (genitalia slide: Mey 11/04), North Thailand, Nan Province, Pua, Doi Phu Kha, 1600m, km 35, 16. – 20. 2. 1993, lux, leg. W. Speidel, deposited in ZMHB (holotype) and coll. Speidel (paratype).

Description (Fig. 1 male, fig. 2 female): Length of forewing 12 mm (male) – 14 mm (female). Head and thorax yellow-white, scape of male with curved processus and enlarged antennal flagellomeres. Tegulae with brown spots. Legs yellow, tarsal segments of foreleg brown at the articulations; femora and tibia of forelegs dark-brown on inner side; male hindfemora with scale-brush. Forewing predominantly yellow except the slightly curved, antemarginal white band which is darkly lined on its margins; frontside of costa with dark line; cell between Cu 1+2 and A 1+2 filled with white in the centre, but not lined; disco-cellular bar reduced to a brown, rounded spot at the base of M2 and M3; a similar brown spot in the anal field between anal vein and wing margin. Cu 2 and A 3 present with their basal stems. Male with tuft of broad scales on R before bifurcation with R 5. Hindwing with subapical incision, strongly developed in male, weaker in female; antemarginal white band short, just reaching the marginal spots; short yellow band at the base of the hindwing present; two small marginal, oval, white spots, lined with black scales.

Male genitalia (Fig. 9): General structure as usual in the genus; valvae long, with 3 apical, caudally directed setae. Gnathos slightly shorter than uncus, with 5 subapical, dorsal teeth. Aedeagus without cornuti.

Female genitalia (Fig. 6): Ninth segment shorter than apophyses posteriores; ductus bursae long, beginning with a wide antrum; colliculum laterally sclerotised.

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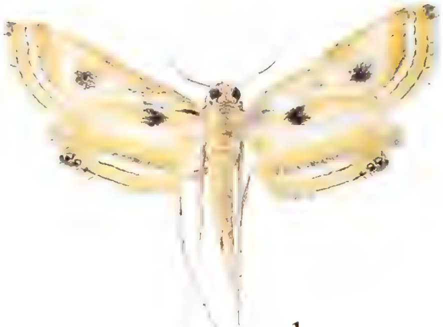
[1] In commemoration of Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004)



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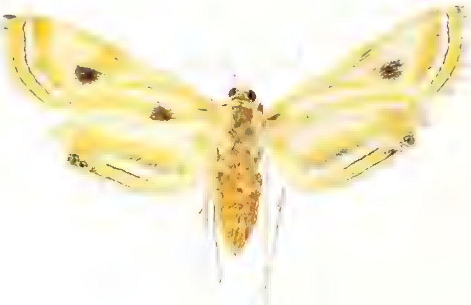

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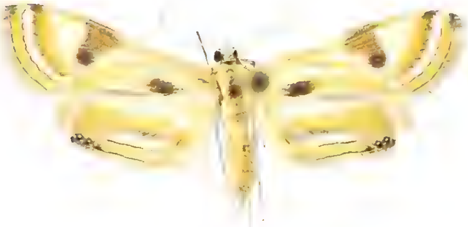

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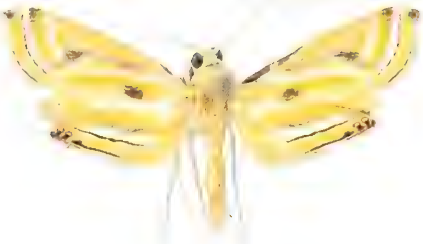

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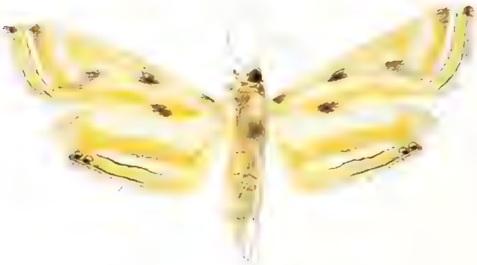

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Fig. 1-5: Adult specimens

Fig. 1: *Eoophyla clasnaumanni* Speidel & Mey sp. nov. Male, paratype. Forewing length 12 mm
Fig. 2: *Eoophyla clasnaumanni* Speidel & Mey sp. nov. Female, holotype. Forewing length 14 mm
Fig. 3: *Eoophyla myanmarica* Mey & Speidel sp. nov. Female, holotype. Forewing length 13 mm
Fig. 4, 5: *Eoophyla aureolalis* (Snellen, 1876) (Indonesia, Sumatra, Sumatera Utara, Prapat, 2°46' N 98°59' E, logging trail 2, 1050 m, 1.-30.12.1994, lux, leg. E.W. Diehl Sumatra), fig. 4 male (Forewing length 9 mm), fig. 5 female (Forewing length 12 mm)

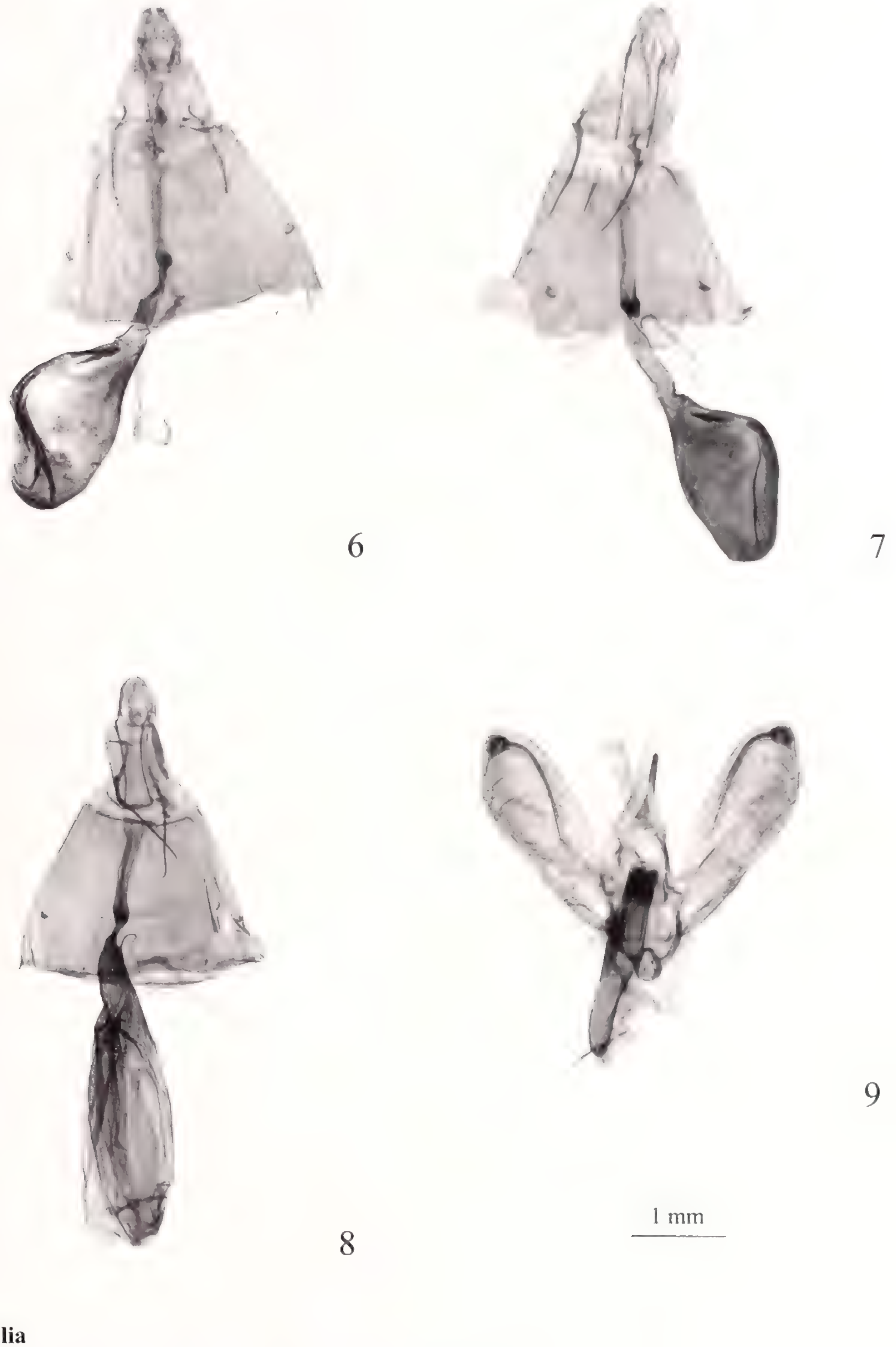

Fig. 6-9: Genitalia

Fig. 6: *Eoophyla clasnaumanni* Speidel & Mey sp. nov. Female holotype.
Fig. 7: *Eoophyla myanmarica* Mey & Speidel sp. nov. Female Paratype.
Fig. 8: *Eoophyla aureolalis* (Snellen, 1876). Female.
Fig. 9: *Eoophyla clasnaumanni* Speidel & Mey sp. nov. Male paratype.

Corpus bursae elongate, club-shaped. Signum consists of small teeths, arranged in one short and one long pair of elongate bands, which are situated on the ridge of the somewhat flattened corpus bursae.

Etymology: The species is named in memory of the late Clas M. Naumann, our distinguished lepidopterist colleague and adviser, who always supported and promoted our studies on Lepidoptera and who passed away far too early.

Relationship: The wing pattern of *E. clasnaumanni* sp. nov. is similar to that of *E. myanmarica* sp. nov. The shape of the corpus bursae and the structure of the signum in the female genitalia are also very similar. They differ, however, in the length of the ninth segment and in the structure of the antrum, being short and wide in *E. clasnaumanni* sp. nov. and long and narrow in *E. myanmarica* sp. nov. Both species probably form a species pair. According to female genitalic structures a related species is *E. simplicialis* sensu Yoshiyasu, 1987, recorded from Thailand.

Eoophyla myanmarica Mey & Speidel, sp. nov.

Material: Female holotype (genitalia slide: Mey 12/04) Myanmar, Chin, Tiddim, Thaing-gnin, 2310 m, 25.5.2001, lux, leg. S. Naumann, deposited in ZMHB. Paratypes: 3 females, same locality, 2200 m, 17.–2.5.2001, lux, leg. S. Naumann, deposited in ZMHB and coll. Speidel.

Description (Fig. 3): Length of forewing 12 mm– 13 mm (females). Head and thorax yellow-white, Tegulae with brown spots. Patagia white. Legs yellow, tarsal segments of foreleg brown at the articulations; femora and tibia of forelegs dark-brown on inner side. Forewing predominantly yellow except the slightly curved, antemarginal white band which is darkly lined on its margins; frontside of costa with dark line; cell between Cu 1+2 and A 1+2 filled with white in the centre, but not lined; disco-cellular bar light brown, but its apex dark brown forming a rounded spot at the base of M2 and M3; a similar brown, slightly elongate spot in the anal field between anal vein and wing margin. Cu 2 and A 3 present with their basal stems. Hindwing with subapical incision, antemarginal white band short, just reaching the marginal spots; short yellow band at the base of the hindwing present; two small marginal, oval white spots, lined with black scales.

Female genitalia (Fig. 7): Nineth segment as long as the apophyses posteriores; ductus bursae long, beginning with a narrow and long antrum; colliculum laterally sclerotised. First part of corpus bursae beyond colliculum a long ductus, widening to a somewhat elongate, trapeze-like form, pleated at the widening. Signum consists of small teeths, arranged in one short and one long pair of elongate bands, which are situated on the ridge of the somewhat flattened corpus bursae; short pair darker than long pair.

Etymology: The specific epithet is derived from Myanmar, today the name of the former Burma.

Relationship: See *E. clasnaumanni* sp. nov.

Eoophyla aureolalis (Snellen, 1876)

Oligostigma aureolalis Snellen, 1876: 193 (key), 200, pl. 8, fig. 5 a-c. Type locality: Java.

Material: 2 ♂♂, 2 ♀♀ (genitalia slide: Mey 13/04), Indonesia, Sumatra, Sumatera Utara, Prapat, 2°46' N 98°59' E, logging trail 2, 1050 m, 1.-30.12.1994, lux, leg. E.W. Diehl (coll. Speidel, ZMHB). Several other specimens, all from Sumatra, in coll. Speidel.

The lectotype, a female, labeled 'Java, Heckmeijer' was selected by Munroe et al. (1958) and is in the Leiden Museum. The lectotype and the only male paralectotype still in Leiden both lack the abdomen (Munroe et al., 1958). The coloured figure in the original description is good and fits very well to our Sumatran specimens.

Description (Fig. 4 male, Fig. 5 female). Length of forewing 8 - 9 mm (males), 10 - 12 mm (females). In comparison with *E. clasnaumanni* sp. nov. and *E. myanmarica* sp. nov. the female of this species has a third, dark brown spot on the forewings. It is situated in the cell before bifurcation of Cu 1a and Cu 1b. The males have a long costal fold in the forewings and the cape is without basal process. The femur and tarsus of the forelegs bear another separating character. In *E. aureolalis* the dark brown, inner and front sides are interrupted by a long, yellow line. The tarsal segments are not dark at the articulations. The yellow line is lacking in the other two species. In the genitalia of the female (Fig. 8), the bursa copulatrix is a large, oval sac, enlarging shortly behind the colliculum. Only a single, elongate, paired signum is present on its ridge. The antrum is wide and the ductus bursae a broad, folded tube.

Relationship: The species of the *crassicornalis*-group exhibit a distinct sexual dimorphism. In general, the females are more uniformly patterned as the males who have developed remarkable, secondary sexual characters. The variety of these traits are not accompanied by appropriate differences in the genitalia. It is therefore difficult to acertain the relationships among species. The wing pattern of *E. clasnaumanni* sp. nov., *E. myanmarica* sp. nov. and *E. aureolalis* show a similar arrangement of spots. It possibly points to a closer relationship of these three species.

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Bonner zoologische Beiträge | Band 53 (2004) | Heft 1/2 | Seiten 121–133 | Bonn, Juni 2005

Of Phenotypes and Genotypes: Two Sides of one Coin in Taxonomy?[1]

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Abstract. We discuss the recent proposals of DNA taxonomy and review some of the basic principles necessary to assess the importance of promoted ideas. We try to show that distinctness and independence of species taxa do not necessarily correlate, at least in newly formed species, which limits the applicability of any applied pattern analysis method. We do not intend to dismiss DNA based taxonomy, but would like to emphasize that molecular characters pose completely new problems to taxonomy often not appreciated enough in the discipline. DNA taxonomy is currently promoted because of its potential for automation. We show that species identification and circumscription can not be entirely automated since the result of a species description in taxonomy is equivalent to the formulation of a locally valid hypothesis. Consequently, every delimitation of a species taxon is open for empirical falsification only on a local scale. It is impossible to extend locally derived criteria, a species delimitation based on criteria derived from single sister species, to a global scale without sacrifying relevant information. We show from a pragmatic perspective that specimen assignment based on molecular characters can be automated under restricted circumstances employing character-based approaches.

1. INTRODUCTION

Several recently published articles advocate the incorporation of molecular techniques into taxonomic protocols (for example HEBERT et al. 2001, 2004; TAUTZ et al. 2002, 2003; STOECKLE 2003, to name just a few). For many practicing taxonomists the incorporation of molecular data seems highly desirable. Without any doubt, the incorporation of as many different character sets as possible into a species taxon description will improve the fit between species taxa and real evolutionary units. What is new in recent articles advocating DNA taxonomy is the emphasis on molecular techniques over morphological approaches, which, as the authors claim, would be the only way to meet the challenges in taxonomy of the 21st century. This is indeed slightly contrary to the perception of taxonomic practice of many taxonomists and aroused obvious opposition.

"Let's face it, the morphological approach has had 250 years to advance the task, and we're only 10% of the way towards the goalposts" said HEBERT in a report on *BioMedNet News*. His solution, to which many taxonomists are strongly opposed, is to distinguish between species on the basis of similarities and differences in their DNA. If taxonomists fail to embrace molecular technology, HEBERT is clear about the consequences: "There is no more likely death of a discipline than the failure to innovate." (HEBERT, BioMedNet News, DNA: the barcode of life? 8 January 2003)

It is certainly true that taxonomy still faces a major task. It has been estimated that only one tenth of assumed existing species has been recognized and described so far. Considering the long tradition in taxonomy, which has been conducted over centuries, this is not really encouraging. Taxonomists estimate that hot spots of biodiversity, tropical rain forests, and also deep sea biotas are still only fragmentarily known. The biodiversity of tropical rain forests is threatened by massive destruction and consequently eradication of largely unknown biodiversity. In many densely populated areas, like Europe or Africa, massive anthropogenic destruction has left deserted areas with presumably significant loss of species and biodiversity. It is comprehensible that taxonomy has to search for ways of speeding up the process of identifying and describing species in the face of these challenges. Here surfaces the second conundrum. Taxonomists generally feel underfunded and it appears that the profession is a vanishing one among biologists. It is hard to find students interested in taxonomic activities, and for several invertebrate groups specialists are already absent. Consequently, training in taxonomy is not being provided, further promoting the loss of knowledge and momentum. Traditional taxonomy thrives from the life-long experience of specialists with trained intuition. The delimitation of species taxa by dedicated specialists and their intuition is often inaccessible for the outsider, making the process of species description quite mysterious. There is no single character with which species taxa can be recognized across phyla. The taxonomic challenge is the discovery of the relevant individual criteria given a population of individuals. Consequently, taxonomists are sometimes seen outside of the realm of natural sciences presenting themselves as book keepers of mental projections. This seemingly subjective and highly artificial approach to recognizing taxa often intimidates the novice student.

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[1] In commemoration of Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004)

Another immanent problem is the publication process in taxonomy. Currently, species descriptions are most often not placed in peer reviewed journals and do not enjoy a high standing among many biologists. It would be ill advised for students hoping for a respectable career to enter the field of taxonomy. As can easily be envisaged, a massive brain drain away from taxonomy is the result.

Among others, molecular taxonomy has been proposed to cushion this development.

But what could be the advantages of using molecular techniques in taxonomy?

The advocates of DNA taxonomy, as it is also called, claim that the genotype provides a universal code with which species could be automatically identified and classified. This indeed seems to draw taxonomic investigation out of the realm of mystery and subjectivity. Automatic detection of species taxa based on genotypic differences would draw taxonomy out of its classroom corner and would transfer taxonomy to a technical enterprise solely executable by machines (TAUTZ et al. 2003; GASTON & O´NEILL 2004).

It is indeed true that the composition of DNA presents a universal resource of variation by the combination of only four character states. Including the phenomenon of indels (a composite word derived from insertion and deletion), we have five clearly distinct characters states with which we can discriminate between DNA sequences. Consequently, genotypes offer the potential of automatic detection of differences between DNA sequences. Different to the plethora of morphological variation, this seems indeed a big advantage as it might alleviate the problem of educating taxonomic specialists. Computers are inexhaustible co-workers doing the job while we are sleeping.

Proponents of DNA taxonomy claim that the simplicity of molecular characters help to solve the problems with which current taxonomy is confronted. Specialists are not needed anymore and identification of new sequence groups can be computerized, greatly speeding up the process of describing the nine-tenths of the unknown biodiversity. It has been already put forward that the description of new species must include a mandatory analysis of selected target sequences thus giving a barcode (HEBERT et al. 2001) of every newly described taxon. To be fair, we have to note that most proponents of DNA taxonomy do not call for a complete disregard of phenotypes but instead argue for a priority of the genotype in species descriptions. Once a species taxon has been recognized based on genotypes, the corresponding phenotypes should be recorded afterwards completing species descriptions (HEBERT et al. 2001; TAUTZ et al. 2003). In other words, the shift from phenotypes to genotypes could provide the answer to the current taxonomic challenges.

In this essay, we will try to sort potentials and pitfalls of the molecular approach in taxonomy. We are particularly interested in theoretical implications, which are surprisingly often omitted in the actual discussion. We will not discuss political implications which have been put forward (LIPSCOMB et al. 2003; MALLET & WILLMOTT 2003) and we will also refrain from discussing the developments in internet technologies which are often promoted concurrently with matters of DNA taxonomy (GODFRAY 2002; SEBERG et al. 2003). Our starting point is a taxonomy which seeks the description of evolutionary units, characterized by reproductive isolation. In this sense, taxonomists try to delimit species taxa by matching phenotypic and possibly genotypic classes with these evolutionary units. This prescription differentiates the taxonomic activity from a mere classification of biological variation for our convenience and text books. DNA taxonomists claim that the genotype is better suited for the delimitation of species taxa matching evolutionary units than any other biological properties of organisms. This proclamation is the focus of our analysis. Consequently, we will first review the principles of genetic variation and variability. Second, we will spend time to review the role of species in evolution. We will not review all of the ideas once promoted but instead give a biased view on what species and speciation probably are and is. Taxonomy as a discipline is often surprisingly ignorant of theoretical issues behind species definitions and the process of speciation. Third, we will discuss the inherently assumed parallelism of character distinctness and population independence, which is at the theoretical foundation of taxonomy in general. But we will also try to show where DNA taxonomy can indeed help to recover lost ground in describing and (re-)identifying specimens. Finally, we will develop ideas of how to incorporate molecular and morphological methods in an automatic way. A final word: we do not claim to present radically new ideas about the incorporation of molecular techniques in taxonomy, but instead try to draw the reader's attention to the limits of DNA based approaches. This is by no means intended to damn DNA taxonomy or glorify the proposals. We feel that the ongoing discussion on DNA taxonomy and taxonomy in general is becoming unbalanced with a strong impetus towards political points of view instead of scientific reasoning.

2. INTRA- VS INTERSPECIFIC VARIABILITY/VARIATION

Considering genetic consequences of speciation, one has to ask how many, what kind of, and in which rate genomic organization of loci change during the process of speciation. Observed genetic differences between species may accumulate not only during or after the speciation process when populations have become independent, but also within populations in terms of intraspecific variation. In the following, we will use the term 'variability' to designate the differences actually present between individuals within a species. The term 'variation', which is often used in a synonymous way, is used to describe differences of individuals of different species.

2.1. Intraspecific variability

As DNA-Taxonomy is often conducted on mtDNA sequences, we will concentrate on the evolutionary patterns of this DNA type, which is nevertheless quite similar to genomic DNA with the exception of its usually maternal inheritance and its haploid occurrence. Genetic differences, as mentioned before, result from four different nucleotides, conventionally symbolized A, T, G, and C. These four character states (or rather five by counting indels) are potentially assumed at each position given enough time for substitution to occur. Genetic differentiation occurs not only between subspecies or species but also within populations as populations are affected by mutation, migration, random genetic drift and natural selection (HARTL & CLARK 1997). Mutation is the source of genetic variation, which arises and increases divergence between mtDNA genotypes. The input of mutations creates and maintains a certain degree of variability within populations (AVISE 2000). Within finite populations in sexually reproducing organisms, new mutations can become fixed after some time without the effect of selection. The rate at which random genetic drift changes allele frequencies or haplotypes varies inversely with the effective population size (N_e) (WRIGHT 1931; FISHER 1930). The smaller a population, the stronger are effects of random genetic drift and the faster the populations will loose its genetic variation. The effective population size is much smaller for mtDNA than for genomic DNA because of its haploid state and its generally maternal inheritance. Now imagine a population with a large distributional range. Gene flow within this population is restricted and consequently, it will be geographically structured. This will affect genetic differentiation between demes (defined as geographical units within which mating is effectively random). The degree of differentiation depends not only on the effective population sizes of demes but also on the pattern of gene flow among them (WRIGHT 1951). Given a finite Mendelian population, which splits into allopatric subpopulations we can expect to see genetic differences within several loci after a certain number of generations without the force of natural selection. The consequence is genetic variability between populations driven by chance. In addition, natural selection plays a role in differentiation between populations of a widely distributed species. Let us assume the beginning of a speciation process within such a species. If populations become separated, genetic variability will be inherited to subpopulations. In this situation, haplotypes within subpopulations are potentially paraphyletic or even polyphyletic (FUNK & OMLAND 2003). Until monophyly of haplotypes will be achieved time must pass by, at least more than $4N_e$ generations, as estimated in simulations (AVISE 1987). Lineage sorting refers to a related problem. A reciprocal monophyly of haplotypes will be generated after complete lineage sorting has been achieved (ENGLBRECHT et al. 2000; cf. below).

Not in every case of recent speciation events do genetic distinctness and population independence go in parallel. We intuitively assume that the formation of species will arrange the total amount of genetic variation among them into non overlapping packages of genetic variation. This assumption is indeed appealing, but not necessarily realized. DNA taxonomy has to deal with issues of population genetics, as it often relies on presumably selectively neutral gene loci. Paraphyly of selectively neutral haplotypes or the absence of genetic differentiation among those pose major problems to taxonomy and clearly restrict the applicability of molecular tools. Imagine speciation events, which lead to a clear differentiation of phenotypes due to, for example, sexual selection but without fixation of selectively neutral alleles in species taxa, because either populations had been large or there was no time yet to fix allele frequencies. The incongruence of genetic and phenotypic distinctness is not an artificial construction. Examples are given by TAUTZ et al. (2003) who mentioned the situation of the African great lakes cichlid fauna. In Lake Victoria, cichlids are strongly differentiated in phenotypic groups but lack a clear genetic differentiation in sequenced mitochondrial markers (MEYER et al. 1990, compare also TAKAHASHI et al. 2001). These considerations illustrate the limits of DNA taxonomy quite nicely; since, despite reproductive isolation, there must be enough time to build up genetic variability between populations.

2.2. Interspecific variation

The degree of genetic differences between populations, subspecies, or species can be described by using genetic distance methods (e.g. NEI 1978). Dealing with a certain degree of differentiation between populations, some researchers are going to classify species by the percentage of genetic divergence (for example MALTAGLIATI et al. 2001; JIGGINS & DAVIS 1998). This requires a constant rate of sequence differentiation at neutral loci, which is independent of population genetic factors mentioned above. However, the influence of small population sizes on the rate of evolution (OHTA 1976) was assessed in a study by DE SALLE & TEMPLETON (1988). They compared interspecific levels of sequence divergence within a *Drosophila* taxon, comprised of several species, supposed to be generated by a founder event and another *Drosophila* taxon, again comprised of several species, which were thought to have originated from a large population. They showed that the second species group presented a much less pronounced molecular differentiation then the first one. Another example in which intraspecific sequence divergence is as great as such among distinct species is given by WAYNE et al. (1990) who analyzed genetic distances of Jackal populations. In summary, the degree of genetic differences will not always match the biological species status one to one. It is indeed tempting to say that there is still a rough correlation between genetic distance and extend of reproductive isolation. If this holds true, a convention on a minimal distance measure could be successful in identifying new species. Alpine snails of the species *Arianta arbustorum* (HAASE et al. 2003) show COI haplotypes of more than 20% differences within a population. A genetic distance of 20% as a general convention to delimit species is useless in many other taxa. This issue will be taken up later again.

3. SPECIES AND SPECIATION

"The primary aims of taxonomy are to name, circumscribe, describe and classify species" (SEBERG et al. 2003, p. 63). We probably all agree that the generation and maintenance of biodiversity is closely linked with the establishment of evolutionary units and our understanding of the processes will rely on our ability to recognize these evolutionary units. In sexually reproducing organisms, species are exactly those evolutionary units without which biological diversity is only incompletely understood. It is therefore paramount to reflect what processes lead to the formation of evolutionary units and what characteristics can be used to identify them. The discussion on species and speciation traditionally includes the following questions: 1) What are proper species definitions and what is the ontological status of species? 2) What are reproductive isolation and isolating mechanisms? 3) What is the predominant mode of speciation and why are there species? We add the taxonomically relevant question of how species are best classified. Subsequently, we will pick up the issues and comment on them from the perspective of a taxonomist. The history of species definitions is legacy. MAYR (1982) gave a most authoritative and readable account on species definitions in taxonomy and evolutionary biology. Definitions are either acceptable or not, but do not represent explanations of the more or less distinctly separate arrays of organisms (DOBZHANSKY 1937). We think that the disputes over proper species definitions are not interesting and we will not follow up this route. Secondly, we will deliberately omit the discussion whether species are classes, natural kinds, or whether species constitute individuals (for a review, see again MAYR 1982). The discussion on the ontological status of species is not important here. (However, it is clear that the question of whether species constitute natural kinds or individuals is much more interesting than disputes over definitions as it confronts us with a problem in need of an explanation). With the modern synthesis in evolutionary biology, species in sexually reproducing groups of organisms are seen as groups of individuals constituting the largest possible inclusive Mendelian population (DOBZHANSKY 1935, 1937). In contrast to prevailing typological species concepts, representatives of the modern synthesis shifted the emphasis from patterns to processes. Inclusive Mendelian populations do not exist in parthenogenetic and asexual organisms and therefore, the term species in the biological sense is not applicable for these groups of organisms. Many taxonomists and natural scientists felt this limitation of the biological species concept as much too restrictive and opted for more inclusive concepts covering also asexuals and parthenogenetic forms. To our knowledge, the most farfetched example is the general lineage concept of species, which applies the term population to sexual and asexual groups of organisms (DE QUEIROZ 1999). We will restrict the term population to a group of sexually reproducing organisms; anything else blurres the essential differences and produces the illusion of unified theories of species. Of course, taxonomy is also dealing with asexually reproducing individuals, but for now, we will deliberately exclude asexuals and parthenogenetics from our discussion.

The formulation of the biological species concept shifted the emphasis from definitorial problems to real scientific inquiry. As DOBZHANSKY put it so easily the reasoning runs as following: first is the observable pattern of distinctive separate arrays of organisms and secondly there is the theory that these separate arrays seem to be maintained by established reproductive barriers between groups. Mayr added a new twist to this theory. He concluded, starting from the question of how characters can evolve despite mixing of genotypes in sexually reproducing organisms, that the formation of Mendelian groups which are reproductively isolated against other such groups should be clearly advantageous. The new twist is the explicit inclusion of the phenomenon of selection albeit in a slightly diffuse way. MAYR was not the first emphasizing isolating mechanism in defining species. Credit has to go to DOBZHANSKY who introduced the term isolating mechanism in his book *Genet-*

ics and the Origin of Species (1937) (The idea of recognition of "proper" reproductive partners is central to species and even much older. It finds its explicit predecessors in Buffon (in MAYR 1982).) DOBZHANSKY (1937) reserved an entire chapter for the discussion of isolating mechanisms. He mentions that "Darwin and Lamarck pointed out that interbreeding of groups of individuals, which are hereditarily distinct, results in dissolution and swamping of the differences by crossing." (DOBZHANSKY 1937, p. 228). He correctly notes that the statement is somewhat misleading since single allelic differences will not diffuse in crosses but segregate again in the offspring. Only distinct character complexes of polygenic origin can break down in crosses leaving the hybrids less competitive compared to parents. For DOBZHANSKY, isolating mechanisms are mechanisms, which prevent the production of hybrid zygotes reaching the reproductive stage. Most importantly, citing Mayr again, isolating mechanisms are seen as "biological properties of individuals which prevent the interbreeding (fusion) of populations" (MAYR 1970). Therefore, sole geographical isolation of populations does not constitute a necessary and sufficient criterion for recognizing reproductively isolated species. The basic principle behind this idea is the insight that Mendelian populations are the units of evolution. (It is interesting to see that the origin of panmictic populations is not important in this respect.) Scientists like DARWIN, LAMARCK, DOBZHANSKY, MAYR, and many more have been convinced that differential adaptation to heterogeneous environments and ecological needs would have been impossible without the partitioning of panmictic populations. For that reason, we can call species independent modules in the evolutionary process.

An analogous picture can be drawn from the field of developmental biology. There it became clear after ground breaking work starting in the early 20th century (BERTALANFFY 1932; WADDINGTON 1957) that evolvability of complex characters can only be maintained by reducing pleiotropic interactions. For example, imagine genes, which effect the formation of epithelia. Specific alleles might promote the formation of a thick keratinous outer layer, thus reducing the risk of dehydration in dry habitats. This could clearly be an advantage for the bearer of this allele. However, thick keratinous layers on bronchial epithelia are certainly counterproductive as they restrict the intake of oxygen. The pleiotropic interactions prevent the fixation of an allele in this case. The situation leads to a reduced adaptability under strong pleiotropic interactions. The solution is the break up of pleiotropic interactions and the recovery of adaptability. The break up of pleiotropic interactions results in the formation of genetic and developmental units, which we also can call modules. The evolution of modules is the key invention (compare for example RIEDL 1978; BONNER 1988; RAFF 1996; WAGNER 1996; WAGNER & ALTENBERG 1996). Similarly, species can be seen as genetically independent modules protecting their harmonious gene pool and thus, maintaining distinctness. The biological species concept refers to exactly these properties of inclusive Mendelian populations. Biological species are characterized by distinctness and independence. Whether distinctness or independence comes first is asking for the priority of the chicken or egg. MAYR himself favored for a long period allopatric speciation processes as the predominating mode of speciation, which implies that independence is acquired first and distinctness is a secondary phenomenon. MAYR's idea predicts a linear order of phenomena from geographic isolation to reproductive isolation. However, theoretical considerations suggest that parapatric speciation and its derivatives (peripatric up to sympatric speciation) are at least conceivable, which makes the decision less obvious (TURELLI et al. 2001).

Polytypic species are species in which individual subpopulations can be characterized by clear phenotypic differences, often given subspecific rank. It is assumed that a reduction of gene flow between geographically distant populations maintains local differences. However, most of the genotypic composition within the species is still homogeneously distributed throughout the entire range. Such a situation is also found in species with clinal variation along an ecological gradient. This even distribution of phenotypic variation can be stabilized by the effects of natural selection, resulting in local fixation of alleles under stabilizing selection (local adaptation). However, selectively neutral alleles will travel freely across large ranges (DIECKMAN & DOEBELI 1999; DOEBELI & DIECKMAN 2003). In such a case, partial independence due to restricted vagility of individuals is driving the evolution of distinctness despite the absence of reproductive isolation. This example illustrates that reproductive isolation is neither a sufficient nor a necessary condition for adaptive change in populations. Local adaptive changes can be accomplished by the action of natural selection alone, even under para-(sym)patric conditions (DOEBELI & DIECKMAN 2003). *Speciation* is the maintenance of phenotypic differences by means of reproductive isolation. Reproductive isolating mechanisms are biological properties of individuals preventing the fusion of gene pools. A compatible definition would be "biological properties, which lead to the interruption of the gene flow between populations".

In the example given above, a population differentiates along an ecological gradient. This gradual differentiation is maintained by the effects of natural selection. Reproductive isolation is not necessary to maintain the gradual difference. But as soon as, for example, female preferences for certain male characteristics become genetically coupled, the gradual differentiation of phenotypes can be translated into an abrupt change in phenotypic properties within now genetically separated populations. This may eventually lead to reproductive isolation (DOEBELI & DIECKMANN 2003). In such a situation, individual selection favors the acquisition of reproductive isolation. Starting from distinct phenotypes, the acquisition of genetic independence becomes a secondary phenomenon. The example above illustrates quite well that reproductive isolation is not necessarily a phenomenon of single gene loci but is best seen as a feature at the organismic level (compare MAYR 2001; WU 2001; WU & TING 2004). In some cases, only a small number of loci might suffice to lead to complete reproductive isolation, in some cases not. Albeit the notion of harmonious gene pools implies a genome wide differentiation, this is not even intended in MAYR's writings (MAYR 1996). We could formulate that genes responsible for reproductive isolation are taking the lead in the differentiation process of the genotype and it will take some time until unique alleles will be fixed for every locus as soon as reproductive isolation has been acquired. Within sexually reproducing populations individuals will have genes (alleles) in common defining the biological properties of reproductive isolation. We call these "species producing genes". It might indeed be possible to give a comprehensive genetic delimitation of a species taxon if based on these species producing genes (MAYR 1996).

The situation is somewhat different in allopatric populations. Change of allele frequencies are expected to be randomly distributed within the genome assuming comparable selection regimes in allopatric populations. From a theoretical point of view, this process, well known under the term random genetic drift inevitably reshapes the composition of genotypes and gene pools, finally generating incompatible gene pools between allopatric populations; incompatible in the sense that after secondary contact of populations, out-crossing individuals will suffer reduced fitness. The acquisition of species status by random drift is assumed to be slow and probably of polygenic origin. Again, it might still be possible to give a comprehensive genetic species delimitation based on genes causing isolating properties. The phenomenon of genetic incompatibility deserves closer attention since it has been considered as the most important factor of the speciation processes. Random genetic incompatibilities have been called Dobzhansky – Muller incompatibilities (ORR & TURELLI 2002). ORR (1995, 2001) showed that if the number of genetic differences between individuals of separated populations increases linearly with time, the number of incompatibilities should increase as the square of their divergence times. This has been called the "snow ball" effect (ORR 1995). The snow ball effect predicts that we will probably often overestimate the number of genetic incompatibilities between populations responsible for postzygotic reproductive isolation. Therefore, we would expect to see many cases of clear genetic incompatibility in experimental crosses of sister species. This is clearly not the case (compare experiments in CHARLESWORTH 1995). It appears that even an occurrence of multiple bottle necks is unable to produce enough genetic incompatibilities between populations to establish effective postzygotic isolation. This experimental evidence casts considerable doubt on the importance of random genetic drift in speciation and it also sheds some light on the interpretation of genetic variation recorded for selectively neutral marker loci. The experimental results tell us to expect substantial differentiation without postzygotic isolation.

We have reviewed the cases in which "species defining genes" take the lead in the genetic differentiation process of newly formed populations. This does not have to be the case. Depending on speciation rates, selectively neutral loci might even take the lead in the differentiation process without causing reproductive isolation. This phenomenon is quite common and leads to geographically structured gene pools with range limited mitochondrial haplotypes, for example, in the Eurasian ground dwelling fish *Cottus gobio* (ENGLBRECHT et al. 2000): several old lineages of *Cottus gobio* recolonized central Europe and readily mixed where they met. In *Cottus gobio*, genetic distinctness and even monophyly of haplotype groups restricted to geographical areas do not indicate reproductive isolation based on biological properties of the individuals. The above mentioned experimental results and theoretical considerations should caution us in accepting selectively neutral marker loci as ideal tools of DNA taxonomy. However, all of the molecular taxonomic work so far is based on selectively neutral marker loci (compare HEBERT et al. 2001).

4. CHARACTERS: CLASSES AND RELATIONS

Populations of polytypic species and allopatric populations in general, capable of fusing after secondary contact force one to accept that the biological properties of individuals, which prevent fusion of populations, are the hallmark of biological species. Therefore, it would be ill advised to base species delimitations on the recognition of any apomorphic character set shared by a number of individuals. This practice has been introduced by people defending derivatives of the phylogenetic species concept (in MAYDEN 1997; WHEELER & MEIER 2000). It is based on the argument that every reproductively isolated population will evolve autapomorphic character states. This is certainly true in the long run, but completely ignores the initial conditions within reproductively isolated populations. There is clearly a different quality to sets of characters whether they constitute "species producing" characters or not. The phylogenetic species concept does not take into account this difference in character qualities. If different quality of information in characters is ignored, any observed difference gains weight. Representatives of typological species concepts refer to the apparent success in applying typological criteria in delimitating species taxa (compare for example HEBERT et al. 2001). We have already shown that there are many conceivable situations in which DNA based taxonomies will lead to erroneous conclusions.

Reproductive isolation is a quality of relations between populations and ultimately of individuals. This means that character attributes of reproductive isolation are from a different world compared to characters displayed by lets say pinned individuals in an insect collection. Imagine a pinned insect in front of you displaying a certain suite of characters: relatively small and elongated, red with black dots on its back. In the drawer, in which the pinned insect was spotted, we discover several other individuals looking alike. In some other drawers, we manage to locate additional specimens with similar phenotypes. A decent hypothesis would be that all those specimens belong to one species characterized as relatively small, elongated, and red with black dots on its back. We could now perform a thought experiment and search for all other possible combinations of the characters size, shape, and dorsal coloration. For example, we could look for big, stout, black and red spotted insects among the pinned myriads of specimens. This is certainly not the only combination we can think of. Maybe we will even be successful and discover a suite of specimens that look exactly like the predicted organism. If we have been successful, we would have filled the class "big, stout, black and red spotted". Does this imply that classes are real entities and not just projections of our mental condition? All organisms in a class truly display the class defining characters and for this trivial reason there is a first reality to the phenomenon. Nevertheless, there is more to classes of characters. Phenotypic characters are signs of the interaction of phenotypes and the environment, evolutionarily and ecologically. Consequently, a class of characters will share a set of environmental interactions that is definitely real. The causal relationship of form and function in this case enables the prediction of form from function and vice versa. It is clear that the causal relationship of form and function is not a linear mapping in biological systems, but we think that in principle, this statement will hold. In contrast, reproductive isolation as a quality of individual (population) interaction emerges as a character of relation separating two sets of individuals. It is in this sense an emergent quality of organisms with historical-factual properties tied to its bearers. Biological properties of individuals preventing fusion of populations are classes of characters, which can be expected to be mutually exclusive in reproductively isolated populations. Traditional taxonomy tries to identify those classes of characters responsible for the quality of reproductive isolation. By doing this, taxonomists often just intuitively sort and weight characters drawn from the general pattern (classes) displayed by individuals to approximate the phenomenon of reproductive isolation. Our sensory apparatus and experience as taxonomists makes us successful in identifying and circumscribing biological species based on phenotypic characters. This is common sense among taxonomists and accepted outside the taxonomic community as well. It would be fascinating to collect complete genetic information on characters leading to reproductive isolation in circumscribing biological species taxa (see also MAYR 1996), but unfortunately, this would probably be a hopeless activity. The quality of reproductive isolation is not restricted to a general class of phenotypic characters and we can expect all kinds of genotypic combinations in this respect. It is obvious that an automated identification and circumscription of species taxa based on the genetics of reproductive isolation is not feasible in the near future. In contrast, DNA taxonomy tries to infer species taxa from analyzing more or less randomly drawn genetic information. With randomly drawn genetic information we refer to the selection of genetic marker systems, which has until now never been guided by the needs of taxonomy. The inclusion of genotypic characters was traditionally based on economical and technical considerations. The limits of the genetic markers currently in use are easily highlighted. A monophyly of sequenced haplotypes will coincide with species taxa only if there was enough time for the population to complete fixation before the onset of a new speciation event. It is therefore an empirical question whether the application of DNA taxonomy becomes restricted to just "old" or equivalently fast divergence processes. FUNK & OMLAND (2003) estimated the frequency of species-level paraphyly or polyphyly at 23% based on 2319 published reports. This frequent occurrence of paraphyly and polyphyly should warn the DNA-taxonomist.

5. SPECIES TAXON AND SPECIMEN IDENTIFICATION

5.1. Introduction

Species taxa are most properly identified by their species-producing class of characters, called biological properties of the individuals preventing the fusion of populations. This is of course often impossible to achieve. The art in taxonomy is the selection of character sets which come close to that goal. At the phenotypic level, we operate by comparing character sets, weighting the information at hand, and develop a hypothesis about the relevance of different character sets. In an ideal case, we would filter a certain set of characters responsible for reproductive isolation. The hypothesis that the selected set of characters is responsible for reproductive isolation between a pair of species is at least theoretically open for empirical falsification. This is a most important strength of the biological species concept. It separates the biological species concept from all other concepts, which emphasize the population lineage properties of species. The introduction of a historical component in species definitions, like specimens belong to a certain species because they are directly linked with other species by descent, creates an hypothesis which is not directly open for empirical falsification. It is clear that organisms are linked by descent. There is nothing wrong with this. But we are convinced that it is not necessary to jumble explanations of historical-narrative with hypothetical-deductive qualities in delimiting species taxa. It is like mixing of taxonomy and phylogenetic systematics without noticing the essential different qualities of the disciplines. Admittedly, the empirical test is seldom conducted and therefore, most species descriptions have to be regarded as points of views instead of critically evaluated hypothesis. But how can the taxonomic enterprise still be a success? It all rests on the shoulders of the specialists familiar with their group of organisms. These specialists develop a feeling for the relevant characters delimiting species taxa in their groups. The success of the traditional taxonomic method is therefore dependent on life-long experience and intuitive solutions. These are certainly not ideal preconditions for the automated inventarisation of biodiversity.

5.2. Specimen identification by means of molecular tools

In general, DNA taxonomy does not deal with species-producing sets of genes. It could be hoped for that "species-producing genes" are not randomly distributed among at least closely related taxa enabling a semi-automated detection of those genes. But detailed genetic analyses of speciation processes revealed that even among closely related sister taxa of *Drosophila*, species-specific genes greatly vary and can not be compared (see review in WU & TING 2004). The manifold differences in courtship display alone seem to support this view. The contradicting argument might be raised that several studies document a driving force of sexual selection in speciation processes (for example OWENS et al. 1999; PANHUIS et al. 2001; ARNQVIST et al. 2000; MISOF 2002). If sexual selection is fueling speciation, it will mostly be restricted to pre-mating isolation and variation within courtship displays. The extent of phenotypic species-differences should be directly translated into a set of genotypic differences comparable between species taxa. To us it appears that we just do not know enough about speciation genes and comparative analyses of speciation processes. We will have to wait for answers from combined empirical and comparative analyses of speciation phenomena until we can develop subtle hypotheses of the "genic view of speciation" (WU 2001).

In any reproductively isolated group, genetic differences will accumulate. Eventually, genetic differences will become fixed for selectively neutral loci as well. Subsequently, the genetic variation for selected loci will gain characteristic autapomorphic characters. But those populations will not by necessity evolve isolating mechanisms. Again, in delimitating and circumscribing species taxa we need to identify the biological properties of individuals causing reproductive isolation. It is not at all sufficient to show even in a sympatric situation that two subgroups of individuals maintain phenotypic differences independently of sex. Just think of genetically fixed polymorphisms within species, text book examples are some orchid flowers or *Anopheles* mosquitos. Selectively neutral marker loci will not be among the candidates. We refer the reader to the illuminating experimental data on effects of random drift on postzygotic reproductive isolation (CHARLESWORTH 1995). Admittedly, autapomorphic characters of, for example, mitochondrial haplotypes within a clear biological species can be used *a posteriori* to filter specimen identity. This filtering of specimens is equivalent to species assignment. Assignment is restricted in its applicability to situations, in which haplotypes within sister taxa have reached monophyly and diagnostic (autapomorphic) character states (for an empirical analysis compare FUNK & OMLAND 2003). It is important to stress the reciprocal monophyly of sister taxa. It is not sufficient to show that the biological species under consideration shows a monophyletic set of haplotypes. For example, consider the scenario of a peripatric speciation event. We start from a population with a large distributional range with a certain degree of genetic variability. In a peripatric situation, geographically marginal subpopulations might evolve reproductive isolation. Their haplotypes of selectively neutral marker loci will likely be monophyletic. However, the stem population from which the peripatric population became isolated was driven in the status of paraphyly. Nevertheless, individuals from the stem population will remain reproductively compatible. It will take time until the stem population again reaches monophyly for the haplotypes under consideration. The paraphyletic situation in the stem population poses clear problems to specimen identification and assignment. Some haplotypes within the stem population will be more closely related to haplotypes of the reproductively isolated population. The distribution of genetic distances will not correspond with species taxa and consequently, can not be used to infer species taxa. It is particularly surprising that genetic distance measures are advocated in many recent publications for the delimitation of species taxa in phenotypically indistinguishable forms. The character based assignment and identification is the only way to go. If, and only if, a set of diagnostic characters has been correlated with reproductively isolated populations, these diagnostic characters can be used in specimen assignment and identification.

A theoretical example will hopefully illustrate the argument above. Assume we are naïve DNA taxonomists and received an unknown invertebrate larva collected in marine sediments. The assignment of the larva to a known taxon will be of great importance because it can bridge gaps in the analysis of biodiversity. We might use genetic information to assign the larva to a certain taxon for which genetic markers have already been characterized. From this larva, we sequence fragments of three different gene loci and the observed sequence information indicates that the sequences are only 5% different from sequences of specimens within a known taxon. As naive taxonomists, we would very quickly say that the larva is the yet undescribed larva of a new taxon. Another detailed analysis of phenotypes and biological properties of individuals within the species taxon suggests that the species has a very heterogeneous genetic distance distribution within its range. We find that genetic distances are indeed observed between 0 - 5 % within a Mendelian group, but a geographically marginal subpopulation appears reproductively isolated judged from additional evidences. Although, genetic distances within this subpopulation are small and the average genetic distance of this subpopulation to members of the stem population fall within the recorded range of the presumably Mendelian stem population. In this situation, genetic distances will be of no help in specimen identification and assignment. However, if we concentrate our search on the identification of autapomorphic characters, which describe the recently derived reproductively isolated subpopulation, we could circumvent the problem of overlapping genetic distances and paraphyly of the stem population. The likelihood of specimen assignment will depend on the extent of previous sampling within the stem and subpopulations; the better the sampling, the better our chance of correct re-identification (compare POZHITKOV & TAUTZ 2002). POZHITKOV & TAUTZ (2002) developed an algorithm to select ideally suited probes for specimen identification in large through-put-assays. This strategy seems very promising, in particular for small organisms in great abundance. The assignment of specimens will of course obey the rules of probability. A very nice example has been developed by the *www.DNA-surveillance* project. It constitutes a web-based molecular identification of whales, dolphins and porpoises (BAKER et al. 2003). Obviously, this DNA based specimen identification tool has helped to review species descriptions and type assignments in this group of organisms. The taxonomy of cetaceans is plagued by the problem of some extremely rare species for which morphological descriptions are often very incomplete. In this case, DNA based taxonomy has undoubtedly helped clarifying issues.

5.3. Specimen identification by means of phenotypic tools

There are other approaches for the rapid (re-)identification of species beside DNA based taxonomy. One possibility is automated species identification through digital image analysis (WEEKS et al. 1997; WEEKS et al. 1999a, 1999b; WATSON et al. 2004; ROTH et al. 1999; STEINHAGE et al. 1997; STEINHAGE 2000). In this automated approach, images of insect wings (e. g. of moths, bees, and wasps) are used to distinguish between species. Images are analyzed concerning venation, color or scale pattern. The system DAISY (**D**igital **A**utomated **I**dentification **Sy**stem; O´NEILL & GAULD 2001; WATSON et al. 2004), for example, was able to identify 83 % of unknown moth species from wing images. Taken into account that digital images were taken in the field, where light conditions are not always standardized and recorded specimens are moving, this is an impressively high success rate. A similar approach is run by the ABIS (**A**utomated **B**ee **I**dentification **S**ystem, ROTH et al. 1999; STEINHAGE et al. 1997; STEINHAGE 2000) project. Here, images of forewings of bees, are taken and their venation is used to identify species on different hierarchical levels like genus, species group within a genus and species. Both projects have in common that the programs have to be trained with sets of images to have some kind of "experience" in identifying species. Thus, the systems are only able to discriminate between already digital recorded species. The systems are able to re-identify specimens of known taxa, but not able to recognize new species. In consequence, this can lead to misidentifications, as the system always tries to match an unknown image to a species. GASTON & O `NEILL (2004) pointed out that an ideal automated species identification system should be able to reject species identification if similarities to known species in the database are too small. Hence, this could help to identify unknown phenotypes within a set of known species in the future. Please notice, this is not similar to saying that the automated systems can be used for recognizing new species. We suggest that the systems can be used to recognize unknown phenotypic variation, which can then subsequently be evaluated by taxonomists. Further improvements of the systems could include better images, more morphological characters (e. g. images of additional parts of the body like limb or head structures), and a database with information about distribution, food plants, flight time and other biological data (WATSON et al. 2004). The project DORSA (German Orthoptera Collections, RIEDE et al. 2004) is one attempt to incorporate distribution maps, links to collections, images of type specimens, and last but not least sound recordings in a single database. A rapid assessment tool was developed for automated song recognition and a sound library will be established soon. In this case, it is possible to re-identify orthopteran species due to the characteristic song pattern of single species. The integration of the mentioned distributional and biological data allows a verification of the identified species. But again, this effort is primarily suitable for re-identifications and not for recognition of new species since the only way to confirm a specimen as an unknown species is to exclude all other known species, which can be difficult if not all known species are included in the database.

In summary, although auspicious efforts have been made to automate species identification through digital image analysis, it is still a long way to go. Two major aspects have to be emphasized in this context. First, all of the presented computed systems are some kind of semi-automated since the program has to be trained; database establishment and updates as well as verification of recorded species will always remain in human hands. Second, these projects are tools for re-identification and not for recognition of new species. But computer-based routine re- identification systems could be at least a great facility to speed up the re-identification of species in biodiversity research. Of course, if species can only be differentiated by genital morphology, which needs first a preparation step, the automated re-identification system will be again of limited use.

6. CONCLUSIONS

The proponents of DNA taxonomy try to convince that without relying on molecular characters we will not be able to register a significant share of biodiversity in reasonable time. Automated DNA based taxonomy is the key word here. We have tried to argue that taxonomy can not become a robot activity and speed up taxonomy for several reasons. The most important one is that describing species taxa is a scientific activity resulting in testable hypotheses despite the prevailing absence of empirical falsifications. The hypotheses are based on universal theories (species are reproductively isolated groups of individuals) and identified local realizations (species-specific characters causing reproductive isolation). Biological properties of individuals preventing fusion of populations are as numerous as there are biological species and are emergent qualities of species taxa. These qualities can not be predicted and consequently elude an automatic detection. But still, we expect a significant impetus from molecular studies, which analyze genetic variability within and among populations. New data on genetic variability can potentially direct our interests in taxonomic studies if genetic and phenotypic data do not correlate. For example, investigations are published, which report on the application of molecular techniques revealing hitherto masked differentiation among seemingly identical phenotypes (PROUDLOVE & WOOD 2003). Obviously, DNA based methods help to discover patterns of differentiation that are possibly correlated with reproductive isolation. For some groups of organisms, in which morphology will not be of great help, the application of molecular tools can certainly be advantageous and become mandatory. However, similarly to phenotype-based species descriptions, assessments of species status based on molecular characters remain points of view as well and are even more limited in their relevance compared to phenotypic characters. Molecular differentiation based on selectively neutral marker loci is definitively not a test of reproductive isolation between populations. Given a set of "well" circumscribed species taxa, DNA taxonomy will speed up descriptive work in biodiversity assessment in the sense that the number of genetically diagnosable species for a given collection event or area can be automatically recorded. This work will profit from automation since hypotheses testing is not involved. However, recent developments in automatic specimen identification based on phenotypes are encouraging as well. These developments should not become underfunded in competition with molecular tools, because the ultimate application of phenotypic identification seems more versatile than any DNA based method. We emphasize that the current practice of using genetic distances to delimit species is ill advised and should be replaced by character-based methods. We see that DNA taxonomy has its clear limitations in specimen (re-) identifications and species taxa circumscriptions. We should stress that we do not even have a grip on the problems facing the description of the 90% undescribed taxa and we speculate that many of them are not described yet because they are close sister taxa of known species. If this is true we are gearing towards the area in which DNA taxonomy is most limited. We should be aware of this problem.

ADDENDUM

It is clear to us that we largely ignored the distinction between sympatric/parapatric and allopatric situations. Some readers might argue that our argumentions are more or less acceptable in allopatric situations, in which assignment of species status is arbitrary anyway, but are not applicable under sympatric/parapatric conditions.

It is indeed tempting to say that in a sympatric situation at least two unlinked selectively neutral markers, which segregate independently of sex, indicate separate species status of their bearers. We would like to argue that even in a sympatric case just two selectively neutral markers rarely tell us who is who.

Theoretical work shows that in a sympatric speciation process the differentiation of selectively neutral markers will lag behind. But finally, even selectively neutral markers will reach fixation. In this case they can indeed indicate species status. However, we would assume that phenotypic differentiation will be quite apparent as well and DNA taxonomy will tell us what we already guessed. On the contrary, consider a secondary contact of populations. If populations display differentiation, for example ecological or sexual differentiation, reinforcement will further promote the evolution of reproductive isolation. But since reproductive isolation is not absolutely perfect, selectively neutral marker loci can still penetrate species borders. In consequence, well differentiated selectively neutral markers will become associated with the wrong "species" without dissolving species borders. We would expect polyphyly or paraphyly of selectively neutral marker loci in relation to species borders and phenotypic differentiation (equivalent to species differentiation genes) will be the better choice in taxonomy. This is exactly what FUNK & OMLAND (2003) found in roughly 23% of published reports. Without phenotypic differentiation in sympatry, DNA taxonomy based on selectively neutral markers can only help if several selectively neutral marker loci display congruent pictures of reciprocal monophyly. We are not aware of a published report applying these considerations rigorously.

Acknowledgements. We would like to thank all members of the molecular unit of the ZFMK for extremely fruitful discussions. We dedicate this paper to the memory of Clas Michael Naumann who died on the 15th February 2004. His much to early death has taken away a person who has come to the aid of us whenever it was necessary; we have to grow up now without him.

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Bonner zoologische Beiträge	Band 53 (2004)	Heft 1/2	Seiten 135–148	Bonn, Juni 2005

A New Lizard of the Genus *Gekko* Laurenti, 1768 (Squamata: Sauria: Gekkonidae) from the Phong Nha - Ke Bang National Park, Quang Binh Province, Vietnam[1]

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Abstract. We describe a new species of the genus *Gekko* from the karst forest of the Phong Nha - Ke Bang National Park, Quang Binh Province, Vietnam. *Gekko scientiadventura* sp. n. is distinguished from all other *Gekko* species occurring in Vietnam by the lack of dorsal tubercles. From the four species of *Gekko* that do not occur in Vietnam and that have likewise no dorsal tubercles (*athymus, melli, subpalmatus,* and *tawaensis)*, the new species may be distinguished as follows: *G. athymus* has more preanal pores than *G. scientiadventura* sp. n. whereas in *G. tawaensis* both preanal and femoral pores are completely lacking. *G. melli* and *G. subpalmatus* are apparently closer related to *G. scientiadventura* sp. n., but in these two species the nasorostrals are separated from each other by internasals. We provide first data on habitat and natural history of the new species and furthermore provide a key for the Vietnamese *Gekko* species.

Key words. *Gekko scientiadventura* sp. n.; karst forest; taxonomy, natural history.

1. INTRODUCTION

According to BOBROV (1995), six species of the genus *Gekko* exist in Vietnam: *G. badenii* Szczerbak & Nekrasova, 1993, *G. chinensis* (Gray, 1842), *G. gecko* (Linnaeus, 1758), *G. japonicus* (Schlegel, 1836), *G. palmatus* Boulenger, 1907 and *G. ulikovskii* Darevsky & Orlov, 1994. However, according to the investigations of OTA et al. (1995) the occurrence of *G. japonicus* in northern Vietnam (see also NGUYEN & HO 1996) must be regarded as doubtful. Not yet contained in BOBROV's (1995) list is *G. grossmanni* Günther, 1994. SCHLÜTER (1999) claims *G. petricolus* Taylor 1962 to occur in the "triangle of Thailand, Vietnam, and Cambodia", but definite Vietnamese records of this species are - to our best knowledge - still lacking. The incomplete state of knowledge of Vietnam's gekkonid fauna is also highlighted by the recent description (1993-1994) of the three species of the genus *Gekko* mentioned above (for the correct year of description of *G. badenii* see GÜNTHER 1994).

When we started our herpetological investigations of the Phong Nha - Ke Bang karst forest, in the Quang Binh Province close to the Laotian border seven years ago, aside from *Gekko gecko* only three species of *Hemidactylus* were known (ZIEGLER & HERRMANN 2000). During our subsequent studies of the herpetological diversity of this area we were able to record three additonal species in the National Park: *Gehyra mutilata* (Wiegmann, 1834) and an undescribed species of each of the genera *Cyrtodactylus* and *Gekko* (ZIEGLER et al. 2004). The former has been described already by ZIEGLER et al. (2002), but the latter, listed still as *Gekko* sp. by ZIEGLER et al. (2004), will be diagnosed and described below.

Because in the aforementioned papers the Phong Nha - Ke Bang National Park, its herpetofauna and the respective conservation needs have already exhaustively been described, we restrict ourselves in the present paper on the diagnosibility of the new species of *Gekko*.

2. MATERIAL AND METHODS

Voucher specimens are deposited in the Vietnam National University (HNUV), Hanoi, in the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn, and in the personal collection of the senior author (CPHR). Comparative material was provided (cadens according to LEVITON et al. 1985) by the Natural History Museum (BMNH), London, and the Museum für Naturkunde (ZMB), Berlin.

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[1] In commemoration of Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004)

Biometric and scalation characters as well as colour pattern data were evaluated in both living and preserved specimens. Measurements were taken with a dial calipper (to the nearest mm). The following abbreviations are used: a.s.l. = above sea level, SVL = snout vent length, TL = tail length, SE = distance from snout tip to front of eye, EE = distance between hindmargin of eye to hindmargin of ear, HW = maximum head width, HH = maximum head height, HL = head length (from tip of snout to hindmargin of ear). The following scale counts were taken: supralabials (SPL), sublabials (SBL), nasals (N); in direction from rostral to labial: nasorostrals, supranasals, postnasals, internasals (IN); postmentals (PM), gulars bordering the postmentals (GP), interorbitals (IO), ventrals (V), scales around midbody (SB), subdigital lamellae under the first (LT1) and fourth toe (LT4), preanal pores (PP), postanal tubercles (PAT), dorsal scale rows in the middle of the third caudal whorl (S3R). In living specimens symmetrical scale counts were taken only on the lizard's right side. Colouration is described according to the standard plates published by GRALLERT & ROLAND (1960).

3. RESULTS

3.1. Description of *Gekko scientiadventura* sp. n.

3.1.1. Diagnosis. A small-bodied species of *Gekko*. The biggest specimen (captive) has a total length of 154 mm, of which 81 mm are made up of the tail. Habitus slender, head distinctly broader than neck, head and body slightly depressed. Unregenerated tail always longer than head-body length, not constricted at its base, not thickened, slighty depressed. Lateral fold weak, upper side of head, body and tail without tubercular scales. Digits and toes slightly webbed at the base, only interspace between toes 4 and 5 not webbed. All digits and toes, except the inner ones, clawed. 14-17 subdigital lamellae below fourth toe. 5-8 preanal pores. Nostril touches rostral. No internasals. Posterior ciliaries spiny. Upper side yellowish to brownish in life. Dorsally seven large light spots that may be expanded to lateral narrow wavy bands. Tail with 7-10 light crossbands. Gular region and parts of venter marbled.

From all species of *Gekko* known to occur in Vietnam *(G. badenii, G. chinensis, G. gecko, G. japonicus, G. palmatus, G. ulikovskii)*, *G. scientiadventura* sp. n. is invariably distinguished by the lack of middorsal tubercles. For more detailed comparison, also with other *Gekko*-species see below (3.4. and 3.5.).

3.1.2. Holotype. ZFMK 76198, adult male, Figs. 1-3, primary limestone forest, Phong Nha - Ke Bang, surroundings of 17.32 N, 106.16 E, ca. 50-150 m a.s.l., Quang Binh Province, Vietnam, coll. H.-W. HERRMANN, VU NGOC THAN & T. ZIEGLER, 27-29 August 2001.

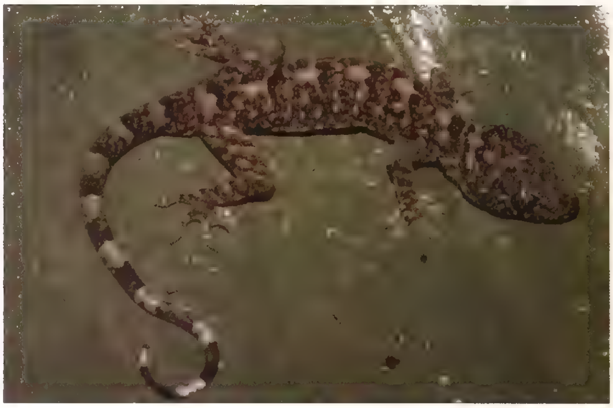

Fig. 1: Live holotype of *Gekko scientiadventura* sp. n. (ZFMK 76198). Phot. T. ZIEGLER

3.1.3. Description of the holotype. Total length 128 mm (for more measurements and indices see Table 1). Rostral twice as broad as high, narrower than mental, without a median suture. 13/12 supra- and 11/10 sublabials. Nostril touches rostral and 1st supralabial. 3/3 nasals, nasorostrals in contact medially. Nasorostrals twice as big as postnasals. Pupil vertical. Tympanum obliquely oval, ca. half of the eye diameter. Interorbital scale count 44. Mental triangular, as broad as high. Two postmentals, twice as long as broad and of subequal length with the 1st supralabial. Postmentals posteriorly touched by six scales. Lateral scales of snout about three times bigger than those on the dorsal side of the snout, roundish, juxtaposed. Head scales granular, ciliaries posteriorly spiny. Gular scales granular, about the same size as upper head scales. Dorsal scales round, smooth, juxtaposed, convex, ca. 1.5 times bigger than head scales. Ventral scales flat, smooth, imbricate, three times as big as dorsals, 41 in an oblique row between the weakly developed lateral folds. Midbody scale count 140. Scales on the upper surface of the upper fore- and hindlimbs flat, smooth and imbricate, granular on the lower. Lower parts of all limbs with granular scales. Fingers and toes basally weakly webbed, only toes 4 and 5 without webbing. 14/12 lamellae under the 1st and 17/15 under the 4th toe. 5 preanal pores arranged in an angularly bent series, 3/3 postanal tubercles. Upper caudal scales flat, subimbricate, as big as the dorsals, arranged in regular transverse rows and weakly expressed whorls, the 3rd whorl being composed of (dorsally) 10 scale rows. Subcaudals flat, smooth, imbricate, 2.5 times wider than high, with a median row of regularly arranged plates; each 3rd plate ca. 3 times as broad as high, marking the beginning of whorl. Laterally, the subcaudals are bordered by alternating scales (2-2-3-2-

2-3-2-2 ...) where scales each are bordering the respective broader subcaudal plate.

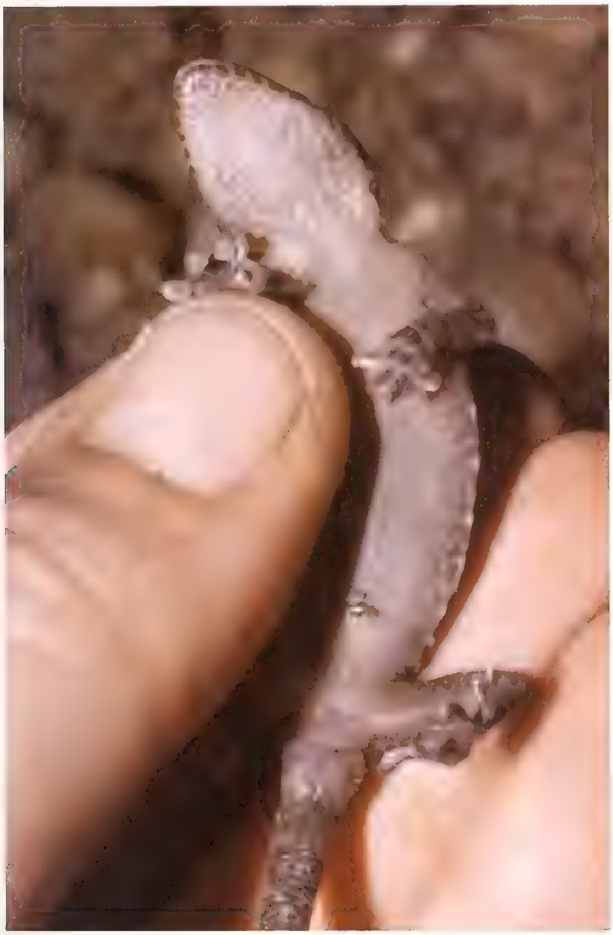

Fig. 2: Ventral view of the live holotype of *Gekko scientiadventura* sp. n. (ZFMK 76198). Phot. T. ZIEGLER

Hemipenial morphology. Right hemipenis (Fig. 3: terminology after RÖSLER 1998) 2.2 mm wide, 4.6. mm long, clavate, forked. Pedicel and truncus not differentiated from each other; basally on the sulcal side is a small wrinkled adminiculum, running laterocranially and not reaching the sperm groove. Above the adminiculum a ribbed area. Apex bilobed, the lobes being subequal in size. Sperm groove originates from the laterocaudal side of the organ and runs straight along the truncus, where it divides into two branches that terminate on the upper side of each lobe in a slit-like concavity. Apically, the sperm groove is shallow and is accompanied by weakly developed sulcal lips. The sperm groove gets deeper and widens towards the proximal part of the truncus. The epidermal tissue of the lobes appears to be rough, although no calyces can be distinguished.

Colour of preserved holotype. Upper side of head and body dark grey. Head grey-brown, with darker vermiculations and flecks, additionally small light dots. Dorsum with seven median light flecks that continue laterally into small transverse bands with strongly waved anterior and posterior margins. These transverse bands are anteriorly bordered by brown-blackish lines and dissolve laterally. Between the single bands light flecks and numerous small spots are interspersed. Limbs above dark grey with grey-brown stripes. Throat, chest and belly buff, the throat bearing a reticulate pattern. Belly laterally with light spots. Forepart of tail above and below dark grey, hindpart grey-black. Nine grey-brown transverse bands on the upper side of tail, the hindmost five reaching the lower side of the tail and nearly form closed rings.

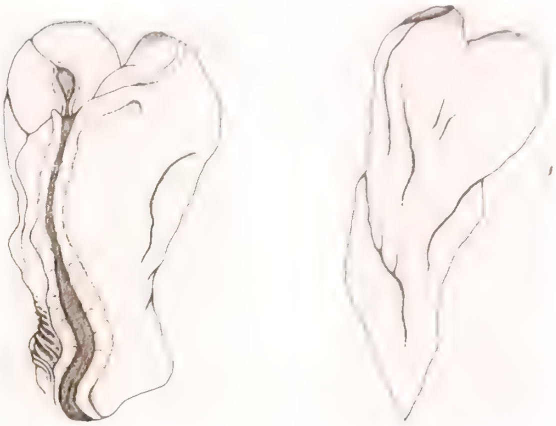

Fig. 3: Right hemipenis of the holotype of *Gekko scientiadventura* sp. n. (ZFMK 76198): a) sulcal, b) asulcal view. Drawing: H. RÖSLER.

3.1.4. Paratypes. ZFMK 76174 (Fig. 4), adult female, ZFMK 76175-179, juveniles, Phong Nha - Ke Bang, surroundings of 17.32 N, 106.16 E, 50-150 m a.s.l., Quang Binh Province, Vietnam, coll. H.-W. HERRMANN, VU NGOC THANH & T. ZIEGLER, 26 August - 1 September 2001. ZFMK 80651-652, adult females, same locality data, coll. VU NGOC THANH & T. ZIEGLER, 29 August - 10 September 2003.

Paratypes ZFMK 76179 and 80652 will be permanently transferred to the scientific collection of the Vietnamese National University, Hanoi (HNUV).

3.1.5. Description of paratypes. Individual body measurements and proportions can be seen in Table 1. For the latter, the paratypes have the following mean values and standard deviations (n being variable): SVL:TL 0.87+/-0.07, SVL:HL 3.49+/-0.24, HL:HW 1.28+/-0.03, HL:HH 2.28+/-0.03, SE:EE 1.33+/-0.09.

All paratypes possess invariably 3 nasals, no internasals and 2 postmentals. Further, females and juveniles are lacking preanal pores. The postmentals are differently shaped, the maximal relative length is the left postmental of ZFMK 76176 which is three times as long as

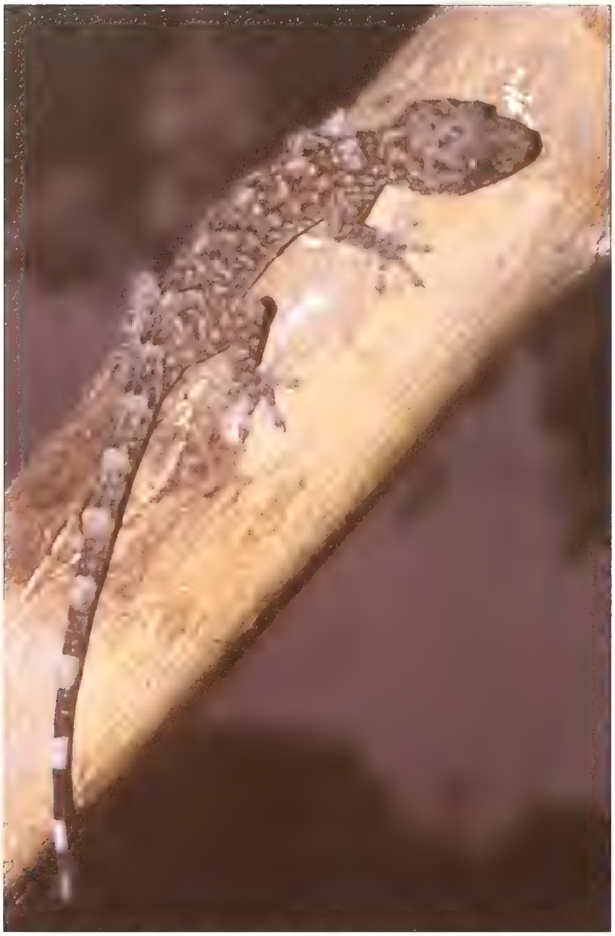

Fig. 4: Live female paratype of *Gekko scientiadventura* sp. n. (ZFMK 76174). Phot. T. ZIEGLER

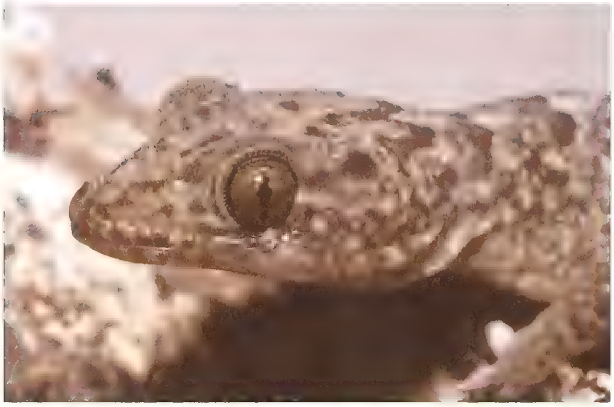

Fig. 5: Portrait of one of the captive males of *Gekko scientiadventura* sp. n. (see also fig. 28 in ZIEGLER et al. 2004) from 22 April 2003, measuring a SVL of 67 mm and a TL of 70 mm at the time; note the spiny posterior ciliaries as well as the bordering nasorostrals. Phot. T. ZIEGLER

broad. The right postmental is divided in ZFMK 76176 and 76178. The posterior ciliaries are spiny in all paratypes. The remaining scalation characters vary to a small degree only (see Table 2). Range (mean and standard deviation) of the number of supralabials is 12-14 (13.00+/-0.82), of the sublabials 9-13 (9.94+/-1.26), of the scales behind postmentals 5-7 (5.67+/-0.71), of the interorbitals 41-49 (43.75+/-3.59), of the ventrals 38-48 (41.80+/-3.90), of the scales around midbody 118-139 (132.20+/-8.23), of the lamellae under the 1st toe 12-15 (13.86+/-1.03), of the lamellae under 4th toe 14-17 (15.64+/-1.15), of the postanal tubercles 2-3 (2.50+/-0.53) and of the number of dorsal scales in the 3rd tail whorl 10-11 (10.29+/-0.49).

All juvenile paratypes (as well as two embryos, see 3.1.6.) have still two egg teeth which touch each other apically as it is typical for geckos with relative thick and calcified eggshells (RÖSLER 2001b). The tooth crown of the egg teeth has a shape similar to that of *G. gecko* (see SLUITER 1893).

Colour of preserved paratypes. The pattern of the preserved material corresponds to that of the living animals, the overall colouration being more greyish.

3.1.6. Other material. Next to the type series, there are two male embryos (ZFMK 76199 and CPHR 2028) and three eggshells (ZFMK 76180) from the same locality. The embryonic males exibit egg teeth as decribed above, their hemipenes are completely everted, deeply forked and show two subequal apical lobes. In one of them (CPHR 8028) the dark pigments (6 crossbands) start to develop.

In addition there are three males and one female (Figs. 5-7, see also fig. 28 in ZIEGLER et al. 2004) that had hatched in September/October 2001 from eggs found in a karst cave at the type locality in August 2001, and which are kept alive in the Cologne Zoo.

3.1.7. Colouration in life. Variable in all adults. Basic colour either more brownish marbled with yellowish flecks, or yellowish with brownish marbling. Upper side of head with large, blackish-brown flecks or spots which may be present also on the snout. Some specimens additionally possess some greyish flecks on the same head regions. Ciliary scales black with yellow margins. Iris metallic green-yellowish, pupil with bronze-coloured margin. A row of 7 middorsal grey flecks which may be extended to wavy crossbands of the same colour towards the flanks. These crossbands may be dissolved into flecks. The middorsal flecks are anteriorly bordered with a blackish brown pattern that is w-shaped in the neck region. The grey crossbars on the tail are likewise anteriorly bordered by blackish brown pattern elements. The grey flecks on the limbs are bigger on the hind legs. Throat and belly with more or less distinct lemon to buff colouration, with more or less distinct brown-olive marbling. Colour pattern of underside of tail variable, with pale or dark grey to ochre or blackish brown flecks.

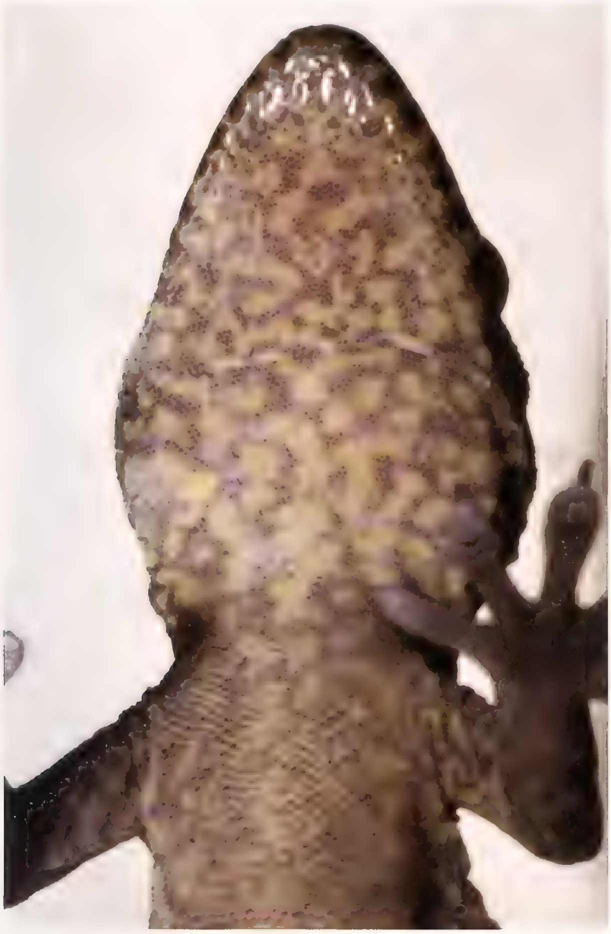

Fig. 6: Gular region of the male of *Gekko scientiadventura* sp. n. depicted in Fig. 5 (10 November 2003). Phot. T. ZIEGLER

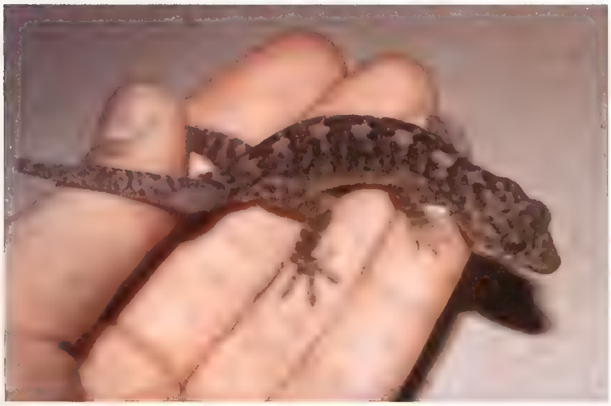

Fig. 7: Captive female of *Gekko scientiadventura* sp. n. (10 November 2003); note the regenerated tail. Phot. T. ZIEGLER

3.1.8. Etymology. The species name is a patronym for a scientific magazine programme of the German Television channel ZDF called "Abenteuer Wissen" (adventure of knowledge) in order to acknowledge the first documentation of the Phong Nha - Ke Bang National Park biodiversity for the German public. First live pictures of *Gekko scientiadventura* sp. n. were shown on this TV programme. The name is derived from the Latin words "scientia" (knowledge, science) and "adventura" (literally = things that will come = adventure) and is a noun in apposition.

3.2. Distribution

So far, *Gekko scientiadventura* sp. n. is known only from the type locality (Fig. 8). Although currently regarded as endemic for Vietnam, its occurrence in Laos cannot be excluded, considering the proximity of the Laotian border from the type locality.

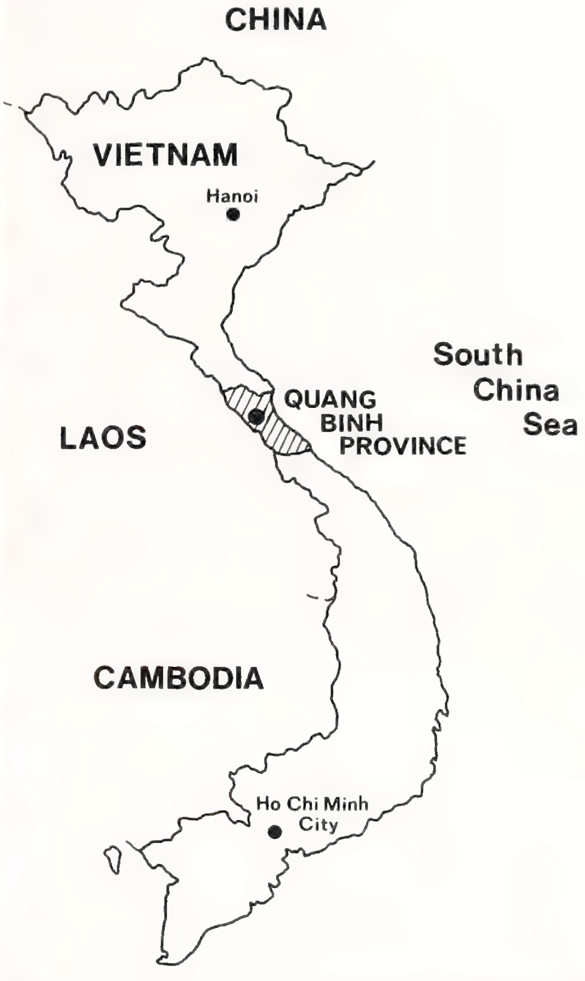

Fig. 8: Position of the type locality within Quang Binh Province.

3.3. Natural history

All specimens of the type series were collected at night in primary forest, either directly on or in the immediate neighbourhood of the karst limestone outcrops that were partly overgrown with vegetation (Fig. 9). The geckos were mostly seen on the vegetation in low height (1.0-2.5 m) rather than on the bare rocks. In contrast, these bare rocks were mostly populated by the syntopic and only recently described bent-toed gecko *Cyrtodactylus phongnhakebangensis* which, in turn, tended to avoid the vegetational parts of the microhabitat (ZIEGLER et al. 2002).

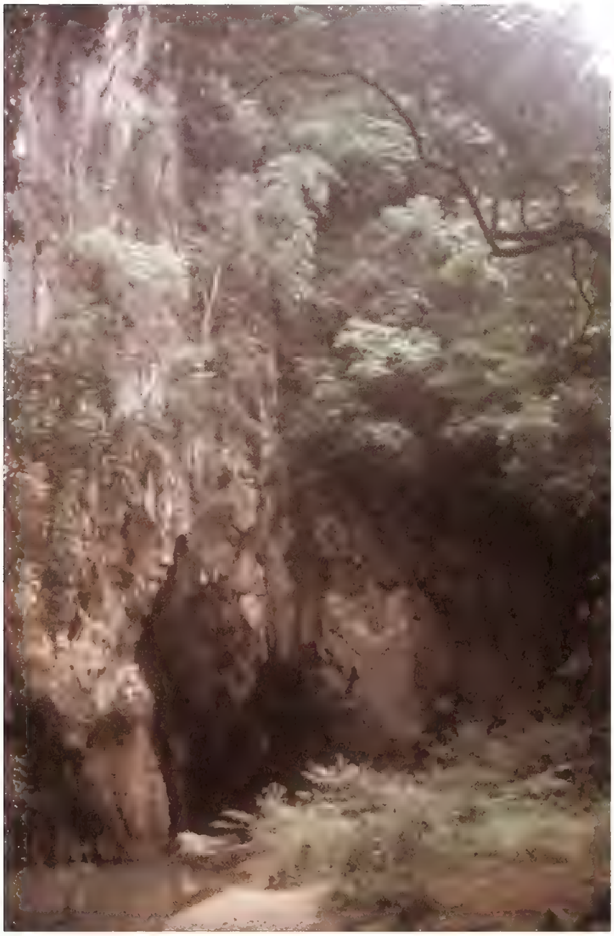

Fig. 9: Habitat of *Gekko scientiadventura* sp. n. near the type locality. Phot. T. ZIEGLER

Apart from the voucher material of our type series no further sightings of *Gekko scientiadventura* sp. n. were made, with the exception of a mass egg-laying site in a dark, manifold rock crevice system at the type locality. Fig. 10 shows this site (in about 2.5 m height) at the beginning of the rainy season (end of August) in 2001. The four geckos cited under "Other material" originate from these eggs; they hatched in September/October 2001 which correlated with the beginning rains. One year later, in August 2003, we found two glued eggs just at this mass egg-laying site. In addition, two further communal egg-laying places were found in this cave system which seemed to be used also already since a longer period; they contained, however, much less eggs and were situated much higher (ca. 5 m high).

On August 30, 2003, we measured at the lower egg-laying site, at 14.30 h, a relative humidity of 85% and a temperature of 27.3 °C. At 21.40 h the same day the temperature was 26.3 °C and the relative humidity had increased to 93% (with a recorded minimum of 70% between 14.30 and 21.40 h). In the primary forest, outside the rock crevice system, we measured with a minimum-maximum thermometer on August 28, 2001 24.4-30.2 °C and one day later 24.3-27.8 °C. For further (long-term) climatic data from this area see HERRMANN et al. (2002).

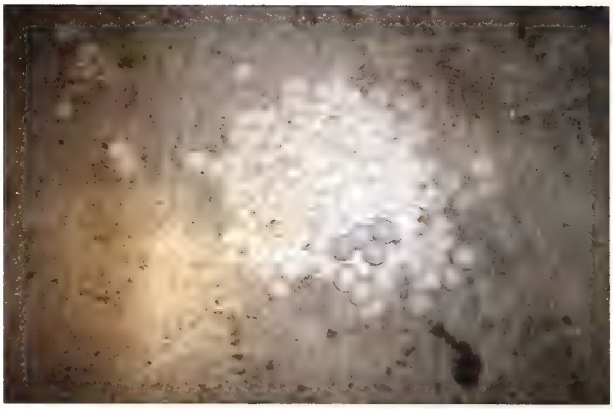

Fig. 10: Mass egg-laying site of *Gekko scientiadventura* sp. n. in a karst rock crevice at the type locality. Phot. T. ZIEGLER

One of the authors (TZ) was able to record some behavioural and autecological observations of the captive-raised geckos: The growling calls of *Gekko scientiadventura* sp. n. were mostly uttered during dawn and night, but could also be heard in summer afternoons (e.g. 22-26 July, 2002), i.e. during the light phase of the terrarium. Obviously, also the black-and-white annulation of the tail plays a role in the infraspecific communication between both sexes, because in an interacting couple the tails were raised and displayed with undulating movements. A male that was taken out of its terrarium used to wag its tail in a much faster manner. Once an acinetic reaction could be observed, a lethisimulation with a recurved tail and extremities that were raised from the ground and standing off from the body. The geckos were fed mainly with crickets of various size classes that were powdered with a vitamin-mineral mixture, however, they were repeatedly observed to lick on and even to bite off small pieces of bananas. In 2003, two egg-layings occured but the paired, partly deformed clutches proved to be unfertilised.

3.4. Comparison with other Vietnamese *Gekko* species

Next to the lack of dorsal tubercles, *Gekko scientiadventura* sp. n. can be distinguished from its Vietnamese congeners by the combination of the characters size, number of internasals and preanal pores as well as dorsal pattern:

G. badenii reaches a SVL up to 76.5 mm and has 1-3 internasals; males have 14-18 preanal pores, and the dorsal pattern consists of 4-8 very narrow and sometimes even interrupted dorsal bands (SZCZERBAK & NEKRASOVA 1994).

G. chinensis (synonym: *G. semipalmatus* Stejneger, 1932) reaches a SVL up to 70 mm. Always 1 internasal which exceeds the nasorostral in size. Males have 18-24 preanal pores. Dorsally 4 indented, cloudy crossbands with light flecks in between (OTA et al. 1995). *G. semipalmatus* has 10 more or less regularly arranged longitudinal rows of dorsal tubercles and the males have 23 preanal pores (STEJNEGER 1932).

G. gecko of Vietnamese origin reach a SVL up to 173 mm. 0-1 internasal. Males have 13-20 preanal pores. Dorsum with transversely and more or less regularly arranged light flecks and dark (brownish to reddish) bands, flecks and stripes (own data). We recognize the following synonyms of *Gekko gecko* (sensu lato): *G. verticillatus* Laurenti, 1768; *G. teres* Laurenti, 1768; *G. perlatus* Houttuyn, 1782; *G. guttatus* Daudin, 1802; *G. verus* Merrem, 1820; *G. annulatus* Kuhl, 1820; *G. indicus* Kuhl, 1857. All taxa considered as synonyms here have (according to their descriptions) dorsal tubercles. We are uncertain in synonymizing *G. aculeatus* Houttuyn, 1782 with *G. gekko* (see also KLUGE 1993, 2001). DAUDIN (1802) considers this name to be synonymous with *Tarentola mauritanica* Linnaeus, 1758 (see also RÖSLER 2001 a). Moreover, we recognize the subspecies *G. g. azhari* Mertens, 1955. Validity and status of *G. reevesii* Gray, 1831 will be discussed elsewhere (RÖSLER & ZIEGLER in prep.). Both last-named forms differ by their size, the dorsal tubercles and the colour pattern unequivocally from *G. scientiadventura* sp. n.

G. grossmanni reaches a SVL of 89 mm. 0-1 internasal. Males with 12-14 preanal pores. Dorsum with several rows of more or less transversally arranged light flecks (GÜNTHER, 1994).

G. japonicus reaches a SVL length of 74 mm and has 1-2 internasals. Males have 6-9 preanal pores. Dorsum with 6 indented dark crossbands which are medially interrupted by light flecks (STEJNEGER 1907; ZHAO et al. 1999; own data). BOURRET (1937) described a male *G. japonicus* from Ngan Son, Tonkin (northern Vietnam) with a SVL of 71 mm as "identique à la description originale, avec une ligne de 10 pores préanaux de chaque côté" (see also BOURRET 1939 and his unpublished manuscript, pp. 34-36). A second locality, Bac Thai, was recorded by NGUYEN & HO (1996). According to OTA et al. (1995), the gecko described by BOURRET belongs to *G. palmatus*. Synonyms of *G. japonicus* are *Platydactylus jamori* Temminck & Schlegel, 1838 and *Hemidactylus nanus* Cantor, 1842. The original description of *H. nanus* contains only notes on the colour pattern (CANTOR 1842), but both types (BMNH 1946.8.26.9-10) have tubercles on back, limbs and tail (pers. comm. C. MCCARTHY).

G. palmatus reaches a SVL of 79 mm and has 0-2 internasals. Males have 24-27 preanal pores. Dorsum including occipital and nuchal region with 6 rows of dark flecks with lighter interspaces (OTA et al. 1995).

G. ulikovskii reaches a SVL up to 108 mm and has one internasal. Males have 10-15 preanal pores. Dorsum with up to eight narrow, light dorsal bands (DAREVSKY & ORLOV 1994).

3.5. Comparisons with the remaining *Gekko* species

According to the original descriptions of all *Gekko* species not occurring in Vietnam, the lack of dorsal tubercles sets *G. scientiadventura* sp. n. unequivocally apart from: *G. albofasciolatus* Günther, 1867; *G. auriverrucosus* Zhou & Liu, 1982; *G. gigante* Brown & Alcala, 1978; *G. hokouensis* Pope, 1928 (synonym: *Luperosaurus amissus* Taylor, 1962); *G. kikuchii* Oshima, 1912; *G. liboensis* Zhou & Li, 1982; *G. mindorensis* Taylor, 1919; *G. monarchus* Schlegel, 1836 (synonyms: *Platydactylus burmeisteri* Giebel, 1861; *P. deissneri* Giebel, 1861); *G. palawanensis* Taylor, 1925; *G. petricolus* Taylor, 1962; *G. porosus* Taylor, 1922; *G. romblon* Brown & Alcala, 1978; *G. scabridus* Liu & Zhou, 1982; *G. siamensis* Grossmann & Ulber, 1990 (synonym: *G. taylori* Ota & Nabhitabhata, 1991); *G. similignum* Smith, 1923; *G. smithii* Gray, 1842 (synonyms: *Platydactylus stentor* Cantor, 1847; *P. albomaculatus* Giebel, 1861); *G. swinhonis* Günther, 1864; *G. verreauxi* Tytler, 1864; *G. vittatus* Houttuyn, 1782 (synonyms: *Lacerta unistriata* Shaw, 1792; *Stellio bifurcifer* Schneider, 1792; *Platydactylus bivittatus* Duméril & Bibron, 1836; *G. trachylemus* Peters, 1872); *G. yakuensis* Matsui & Okada, 1968.

According to the English summary of the Chinese original description of *G. taibaiensis* Song, 1985, this species is closely related to *G. swinhonis* and *G. japonicus* (SONG 1985). From these, *G. taibaiensis* differs by fewer preanal pores (4-6) which are arranged in an interrupted order. The maximum SVL is 69 mm, and there are 7-8 subdigital lamellae under the fourth toe (ZHAO et al. 1999). *G. taibaiensis* differs from *G. scientiadventura* by its significantly lower number of subdigital lamellae under the 4th toe and the series of preanal pores which is medially interrupted by a smooth scale. The specimens figured by SONG (1985) and HUANG & ZONG (1998) do not show a contrasting dorsal pattern as does *G. scientiadventura* sp. n.

There are only few species in the genus *Gekko* that have a lack of dorsal tubercles in common with *G. scientiadventura* sp. n. These are *G. athymus* Brown & Alcala, 1962, *G. subpalmatus* Günther, 1864, and *G. tawaensis* Okada, 1956.

G. athymus reaches a SVL of 100-120 mm, and has one internasal. Digits webbed for 1 third of their length. 19-

21 subdigital lamellae under 4th toe. Males with 22-23 preanal and femoral pores; subcaudals transversely broadened (BROWN & ALCALA 1962, 1978).

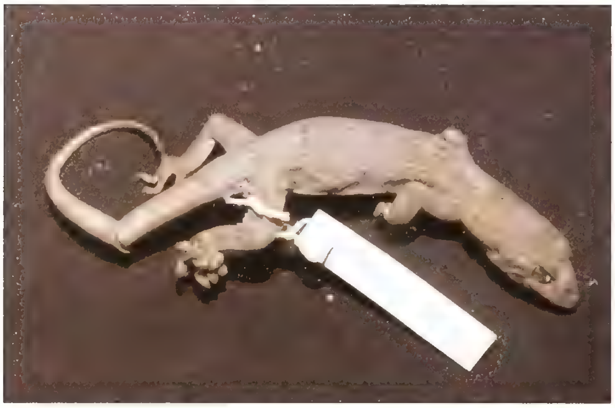

Fig. 11: Dorsal view of the holotype of *Gekko subpalmatus* (BMNH 1946.8.2592). Phot. T. ZIEGLER

G. subpalmatus reaches a SVL of 78 mm and has 1-2 internasals. Toes basally narrowly webbed. 7-10 subdigital lamellae under 4th toe. Males with 5-11 preanal pores. Subcaudals transversely broadened (GÜNTHER 1864; POPE 1935; ZHOU et al. 1989; ZHAO et al. 1999). For a better comparison with *G. scientiadventura* sp. n. we studied the holotype of *Gekko subpalmatus* (BMNH 1946.8.2592) and the lectotype and the paralectotype of *Gekko melli* Vogt, 1922 (ZMB 27659 A & B) which is considered to be synonymous with *G. subpalmatus* (e.g. ZHAO & ADLER 1993) (Figs. 11-13): The rostral of the holotype of *G. subpalmatus* has a short upper transverse suture, the posterior ciliaries are pointed, and there are five distinct tubercles anterior of the tympanum on the right side of the head. The dorsum is lilac-grey to violet-grey, a light postocular stripe and four longish grey-brown vertebral flecks are barely visible, and the tail has several broad light transverse bands that are bordered by darker pigment. The lectotype and the paralectotype of *G. melli* lack a rostral suture, the posterior ciliaries are likewise pointed, and pretympanic tubercles are lacking. The dorsum of ZMB 27659 A is olive-brown. There is a dark naso-ocular and a light postocular stripe. Two dark stripes are running from the ear openings to the axillae, and the shoulder region shows two sepia-coloured stripes. The dorsum has three broad, irregular and partly confluent, grey-brown bands with sepia-coloured margins, the tail has four broad pale brown bands that are likewise bordered by darker pigment. The regenerated tail tip has fine darker dots. Apart from their colour pattern, the types of both taxa differ also in size and in body proportions (SVL/TL index) and in the number of interorbitals, subdigital lamellae under the 4th toe, and scale rows in the third caudal whorl (see Tab. 3). Pending future studies on more material we consider *G. melli* therefore as valid.

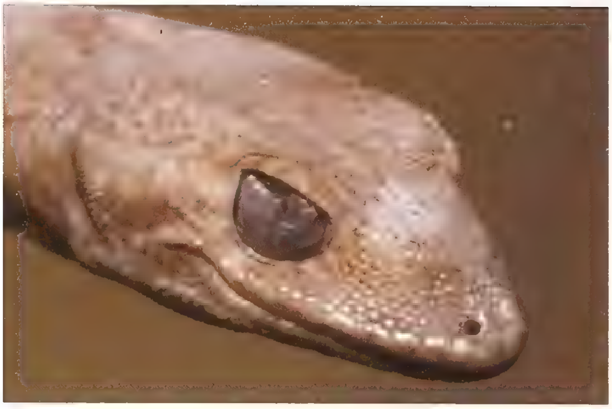

Fig. 12: Portrait of the holotype of *Gekko subpalmatus* (BMNH 1946.8.2592). Phot. T. ZIEGLER

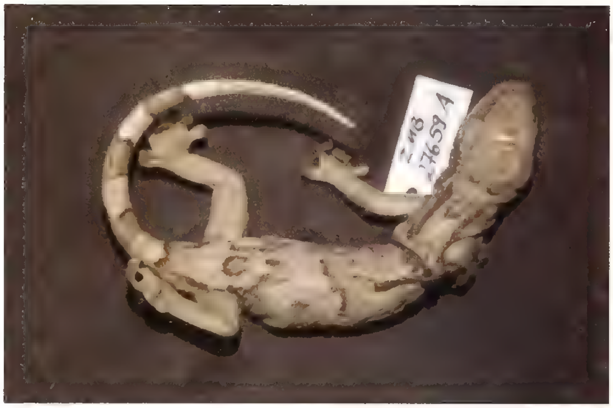

Fig. 13: Dorsal view of the lectotype of *Gekko melli* (ZMB 27659 A). Phot. H. RÖSLER

G. tawaensis reaches a SVL up to 70 mm and has internasals. The toes are basally narrowly webbed, and there are 12 subdigital lamellae under the 4th toe. The males have no preanofemoral pores, and the subcaudals are anteriorly mesially divided (OKADA 1956; SENGOKU 1989; UTSUNOMIYA et al. 1996).

G. scientiadventura sp. n. differs from the other *Gekko* species without dorsal tubercles by the combination of following characters: (a) SVL, (b) internasals, (c) extension of webbing between toes, (d) subdigital lamellae under 4th toe, (e) number of preanal pores, and (f) shape of subcaudals. *G. scientiadventura* sp. n. differs thus from *G. athymus* in the characters a, b, d, e; from *G. subpalmatus* in the characters a, b, c, d; and from *G. tawaensis* in the characters b, e, and f.

4. DISCUSSION

The genus *Gekko* Laurenti, 1768 contains, according to the last overview by KLUGE (2001) 28 species. We add to this number five more species which we consider as valid: *G. liboensis* Zhou & Li, 1982, *G. melli* Vogt, 1922, *G. mindorensis* Taylor, 1919 *G. scabridus* Liu & Zhou, 1982, and *G. scientiadventura* sp. n.

ZHAO & ADLER (1993) formally synonymize *G. liboensis* with *G. hokouensis*. KLUGE (1993), WELCH (1994), MATSUI & OTA (1995) and ZHAO et al. (1999) regard *G. hokouensis* as valid. It has 10 irregular rows of dorsal tubercles and 5-9 rows of prenanal pores (ZHOU et al. 1989; ZHAO et al. 1999).

According to BAUER (1994) who refers to a personal communication by R. CROMBIE, *G. mindorensis* is a synonym of *G. kikuchii*. Both possess dorsal tubercles (TAYLOR 1919). However, *G. mindorensis* has more preanofemoral pores and longer limbs. Moreover, it has broad, medially divided, dark dorsal crossbands (FERNER et al. 2001; GAULKE 2003), whereas *G. kikuchii* has a double series of dark flecks on the dorsum (see the figs. in LU et al. 1999 and in HENKEL & SCHMIDT 2003).

ZHAO & ADLER (1993) formally synonymize *G. scabridus* with *G. chinensis*, whereas MATSUI & OTA (1995) and ZHAO et al. (1999) regard the former as valid. *G. scabridus* has 17-21 irregular, longitudinal rows of dorsal tubercles and 10-15 preanal pores (ZHOU et al. 1989).

The presence or lack of dorsal tubercles does not occur solely in the genus *Gekko*. Also other gekkonine genera, e.g. *Hemidactylus* Gray, 1825, and *Pachydactylus* Wiegmann, 1834, contain species with or without dorsal tubercles (SMITH 1935; FITZSIMONS 1943; LOVERIDGE 1947). The majority of *Gekko* species has these tubercles (SENGOKU 1989). Additionally, species-specific tubercles may also exist on the upper surfaces of head, limbs and tail. The tubercles may be rather big, as in *G. monarchus*, or very small, as in *G. ulikovskii*. Neither their relative size nor their complete absence are geographically correlated. Of the four tubercleless species, only *G. scientiadventura* sp. n., *G. melli* and *G. subpalmatus* are mainland species (Vietnam, southern China), whereas *G. tawaensis* is an endemic of Japan (southern Honshu und some small satellite islands) and *G. athymus* is an endemic of Palawan Island (Philippines).

Apart from the lack of dorsal tubercles, the four species have only few characters in common. The dorsal and tail pattern of *G. scientiadventura* sp. n. resembles most *G. tawaensis* (see fig. in UTSONOMIYA et al. 1996). Also in *G. subpalmatus*, the dorsal pattern consists of medially arranged light flecks, and the tail is banded (see fig. in ZHAO & ADLER 1993). The dorsal pattern of *G. athymus* consists of indistinct, broad, wavy bands (BROWN & ALCALA 1962). However, light vertebral areas or flecks/bands respectively occur more or less conspicuously also in other *Gekko* species (among else in *G. auriverrucosus, G. chinensis, G. hokouensis, G. japonicus, G. similignum, G. swinhonis)* so that closer relationships among the tubercleless *Gekko* species cannot be deduced from this character. Phenotypically *G. scientiadventura* differs among the four tubercleless species most from *G. athymus* which is the geographically remotest (see above). From *G. tawaensis*, it differs by the anteriorly undivided subcaudals. Transversally widened (plesiotypic) versus divided (apotypic) subcaudals are not an exclusive character for *Gekko*, but are also common in the genera, e.g., *Lygodactylus* Gray, 1854 and *Phelsuma* Gray, 1825 (PASTEUR 1964; LOVERIDGE 1942).

A closer relationship of *G. scientiadventura* sp. n. to the two insular species *G. athymus* and *G. tawaensis* seems unlikely to us. Rather, our new species seems to be closer to *G. melli* and *G. subpalmatus* which has to be proven by future (molecular) studies. Both species, however, lack the striking spiny ciliary scales, and they have much broader webbings between the toes. *G. subpalmatus* differs strikingly from *G. scientiadventura* sp. n. by its uniform colour pattern (see figs. in ZHAO & ADLER 1993; HUANG & ZONG 1998). Less uniform is *G. melli*, but its dorsal bands are more roughly shaped as compared with the finely structured dorsal pattern of *G. scientiadventura* sp n.

5. KEY TO THE *GEKKO* SPECIES OF VIETNAM

1	Dorsal tubercles lacking	*Gekko scientiadventura* sp. n.
1'	Dorsal tubercles present	2
2	SVL > 110 mm	*G. gecko*
2'	SVL < 110 mm	3
3	Broad webbing between toes	4
3'	Narrow webbing between toes	5
4	1 Internasal, larger than nasorostrals	*G. chinensis*
4'	0-2 Internasals, smaller than nasorostrals	*G. palmatus*
5	Males with less than 10 preanal pores	*G. japonicus*
5'	Males with more than 10 preanal pores	6
6	Dorsum with blotches	*G. grossmanni*
6'	Dorsum with bands	7
7	30-37 Interorbitals, southern Vietnam	*G. badenii*
7'	40-46 Interorbitals, central Vietnam	*G. ulikovskii*

Acknowledgements. We thank Prof. Vo Quy and Prof. Dr. Truong Quang Hoc (Centre for Natural Resources Management and Environmental Studies, Vietnam National University, Hanoi) for their continuous assistance and encouragement. The People's Committee of Quang Binh, the Forestry Planning Department of Quang Binh and the Phong Nha - Ke Bang National Park administration issued work and collecting permits. We are especially indebted to the National Park director Nguyen Tan Hiep and his vice directors Cao Xuan Chinh and Luu Minh Thanh, as well as Dinh Huy Tri, the director of the Science Research Center. The National Park staff and our guide Bui Ngoc Thanh helped to make fieldwork successful. We wish to thank Dr. Rainer Günther (ZMB, Berlin) and Dr. Colin McCarthy

(BMNH, London) for the loan of specimens under their care. We are greatful to Dr. Ivan Ineich (Muséum National d'Histoire Naturelle, MNHN, Paris), Dr. Hidetoshi Ota (Tropical Biosphere Research Center, University of the Ryukyus, Okinawa) and Dr. Franz Tiedemann (Naturhistorisches Museum Wien, NMW, Vienna) for their support and for fruitful discussions. The field work of H.-W.H. and T.Z. was funded in large by the Zoological Garden Cologne, the Kölner Kulturstiftung der Kreissparkasse Köln and BIOPAT. Last but not least we are grateful to the German Television channel ZDF for supporting biodiversity research and nature conservation in the Phong Nha - Ke Bang National Park.

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Table 1: Measurements and proportions of *Gekko scientiadventura* sp. n. For abbreviations see Material and Methods, Section 2 * = holotype; ** = paratype; *** = live specimen.

	SVL	TL	HL	HW	HH	SE	EE	SVL : TL	SVL : HL	HL : HW	HL : HH	SE : EE
ZFMK 76174**	69.0	78.7	18.2	14.0	8.0	8.2	6.5	0.88	3.79	1.30	2.28	1.26
ZFMK 76175**	35.0	41.5	9.5	7.4	4.0	4.5	3.0	0.84	3.68	1.28	2.38	1.50
ZFMK 76176**	27.0	29.0	8.6	7.0	3.8	3.9	2.8	0.93	3.14	1.23	2.26	1.39
ZFMK 76177**	30.0	36.3	9.0	7.0	4.4	4.3	3.2	0.83	3.33	1.29	2.05	1.34
ZFMK 76178**	29.5	36.0	9.0	7.0	4.1	3.9	3.2	0.82	3.28	1.29	2.20	1.22
ZFMK 76179**	29.0	33.0	8.4	6.4	4.0	4.0	3.0	0.88	3.45	1.31	2.10	1.33
ZFMK 76198*	60.0	68.0	15.5	12.2	5.0	7.7	5.1	0.88	3.87	1.27	3.10	1.51
ZFMK 76199**	26.5	26.5	8.0	6.4	–	–	–	1.00	3.31	1.25		
ZFMK 80651**	66.5	–	17.6	13.4	7.0	8.0	6.5	–	3.78	1.31	2.51	1.23
ZFMK 80652**	59.8	75.0	16.5	12.9	7.0	7.9	5.8	0.80	3.62	1.28	2.36	1.36
male***	70.0	75.0	19.5	15.0	8.5	9.0	7.0	0.93	3.59	1.30	2.29	1.29
female***	68.0	–	18.0	13.5	7.5	8.5	7.0	–	3.78	1.33	2.40	1.21
male***	66.0	70.0	19.0	14.0	8.0	8.5	7.0	0.94	3.47	1.36	2.38	1.21
male***	73.0	81.0	20.0	15.0	8.0	9.0	7.0	0.90	3.65	1.33	2.50	1.29

Table 2: Pholidosis of *Gekko scientiadventura* sp. n. For abbreviations see Material and Methods, Section 2. * = holotype; ** = paratype; *** = live specimen.

	SPL	SBL	N	IN	PM	GP	IO	V	SB	LT1	LT4	PP	PAT	S3R
ZFMK 76174**	13/13	13/12	3/3	0	2	5	41	38	139	12/14	14/14	0	3/3	10
ZFMK 76175**	13/12	9/9	3/3	0	2	6	–	48	118	14/12	17/16	0	3/3	10
ZFMK 76176**	14/13	11/11	3/3	0	2	6	–	43		13/14	15/17	0	–	10
ZFMK 76177**	14/14	9/9	3/3	0	2	5	–	40	133	14/-	15/-	0	–	11
ZFMK 76178**	13/14	9/9	3/3	0	2	5	–	43	136	13/15	17/-	0	–	
ZFMK 76179**	12/12	9/9	3/3	0	2	7	–	40	135	15/-	16/16	0	–	10
ZFMK 76198*	13/12	11/10	3/3	0	2	6	44	41	140	14/12	17/15	5	3/3	10
ZFMK 76199**	14/12	10/9	3/3	0	2	5	-			–	–	0		
ZFMK 80651**	–	11/11	3/3	–	2	6	42	43	131	14/14	15/14	0	2/2	11
ZFMK 80652**	12/13	10/9	3/3	0	2	6	49	42	133	15/15	17/16	0	2/2	10
male***	13	11	3	0	2	5	47	-	-	14	14	6	3	
female***	14	12	3	0	2	7	48	-	-	14	16	0	3	–
male***	13	11	3	0	2	5	49	-	-	14	14	8	3	
male***	14	11	3	0	2	5	51	-	-	14	14	6	3	

Table 3: Measurements, proportions and pholidosis of *Gekko subpalmatus* (holotype BMNH 1946.8.2592, female) and *Gekko melli* (lectotype ZMB 27659 A, female; paralectotype ZMB 27659 B, juv.). For abbreviations see Material and Methods, Section 2.

	BMNH 1946.8.2592	ZMB 27659 A	ZMB 27659 B
SVL	55.0	84.6	29.0
TL	56.0	76.0*	26.5
HL	14.3	22.0	9.0
HW	11.0	15.8	6.6
HH	6.2	9.2	4.0
SE	7.1	9.3	4.0
EE	5.5	8.2	3.1
SVL : TL	0.98	1.11	1.09
SVL : HL	3.85	3.85	3.22
HL : HW	1.30	1.39	1.36
HL : HH	2.31	2.39	2.25
SE : EE	1.29	1.13	1.29
SPL	10/10	11/13	11/10
SBL	10/10	11/12	11/9
N	3/3	3/3	3/3
IN	1	1	1
PM	2	2	2
GP	5	4	6
IO	45	39	35
V	42	43	49
SB	148	147	158
LT1	12/11	11/11	11/10
LT4	10/10	14/12	14/13
PP	0	0	0
PAT	1/1	1/1	1/1
S3R	7	9	9

* 25.0 mm regenerated

Bonner zoologische Beiträge	Band 53 (2004)	Heft 1/2	Seiten 149–163	Bonn, Juni 2005

Analyse der biologisch-ökologischen Ursachen der Evolution der gastroneuralen Metazoa – Testen einer phylogenetischen Hypothese[1]

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Abstract. The goal of our paper is to test the validity of the phylogenetic hypothesis built by AHLRICHS (1995) concerning the evolution of the gastroneuralian metazoa. While phylogenies are historical-narrative explanations of the evolutionary history of groups of organisms, the evolutionary theory and the mechanisms and processes of the evolutionary change are nomological-deductive explanations of the organismic evolution. Because phylogenies completely depend on the working evolutionary mechanisms and processes, phylogenetic hypotheses must be based on and tested against the theory of evolution. Answering the question *"Why are gastroneuralian metazoa?"* requires a functional-adaptive (nomological-deductive) analysis of the key characters evolutionary responsible for building the ecological zone of the gastroneuralian stem species. Those functional-adaptive analyses are an essential part for testing the validity of phylogenetic hypotheses. By our analysis of the key characters of the gastroneuralian metazoa the hypothesis of the monophyletic origin of the Gastroneuralia could not be falsified.

Key words. Gastroneuralia, Bilateria, phylogeny, evolution, nomological-deductive explanation, historical-narrative explanation, functional-adaptive analysis, key characters

1. PROLOG

Wir verfolgen hier das Ziel, die Evolution des Taxon Gastroneuralia (= Nemathelminthes + Spiralia, sensu AHLRICHS 1995) kausal zu erklären. Der geneigte Leser möge jedoch keine vollständige und abgeschlossene Erklärung der Evolution der Gastroneuralia erwarten. Der nachfolgende Aufsatz ist vielmehr als Einübung in eine umfangreichere Bearbeitung des Problems zu sehen.

Die Kausalanalyse der Evolution höherer Taxa umfasst nach BOCK (1981) zwei wichtige Schritte: 1. die Entwicklung einer phylogenetischen Hypothese und 2. die funktional-adaptive Analyse der Schlüsselmerkmale des Taxon, dessen Evolution erklärt werden soll. Vor allem der zweite Schritt – die Merkmalsanalyse – ist von besonderer Bedeutung, da diese einen Test der phylogenetischen Hypothese ermöglicht und die Grundlage für die Abschätzung der Validität der phylogenetischen Hypothese darstellt. Die in den Phylogenien verschiedener Taxa zum Ausdruck kommenden „Genealogien" sind Abstraktionen der zurückliegenden Evolutionsgeschichte. Phylogenien sind daher eine Form von historisch-narrativen Erklärungen (NAGEL 1961; HEMPEL 1965, 1977; BOCK 1981) der Evolutionsgeschichte.

Bei der Rekonstruktion einer Phylogenie treffen wir zunächst auf ein rational-empirisches Verfahren, das nicht kausalanalytisch einsetzt, sondern vergleichend zur Erkenntnis gelangt. Dieser vergleichend formenkundliche Frageansatz beruht auf der abgestuften Gestaltähnlichkeit der Organismen und beinhaltet die Ursachen dieser Gestaltähnlichkeit sowie deren historisches Gewordensein zunächst nicht. Vielmehr arbeitet der morphologische Frageansatz mit der Vorstellung von der Vergleichbarkeit der Gestalten und mit der Möglichkeit, einzelne Arten in Gruppen und diese Gruppen wiederum in umfassenderen zusammenfassen zu können, wobei ein hierarchisch-enkaptisches System entsteht, in dem jede Gruppe durch gemeinsame Gestaltmerkmale gekennzeichnet ist. Die auf diese Weise formulierten Abstammungshypothesen sind, wie alle wissenschaftlichen Hypothesen, theoriebelastet. Seit Charles DARWIN (1859) seine Theorie der organismischen Evolution in seinem revolutionären Werk *On the Origin of Species by Means of Natural Selection* veröffentlicht hat, müssen phylogenetische Hypothesen auf der Theorie der organismischen Evolution begründet sein.

In vielen kladistischen Untersuchungen gehen die Autoren dagegen immer noch davon aus, dass phylogenetische Systematisierung und Evolutionsbiologie voneinander unabhängig sind. Dieser Ansicht scheint auch AX zu sein (1984, S. 59), wenn er schreibt: „Das Verfahren der phylogenetischen Systematisierung von Organismen ist unabhängig von jeglicher Vorstellung über kausale Mechanismen der Evolution, gleichgültig, ob es sich um das Hypothesengebäude der ‚synthetischen Theorie der Evolution' ... handelt, um Erweiterungen und Veränderungen dieser Theorie oder um Alternativen zu ihr...", und er fährt fort (Ax 1984, S. 136): „Die Ordnung der Produkte der Phylogenese und die Wiedergabe ihrer Verwandtschaftsbeziehungen in einem phylogenetischen System ist rational und methodologisch unabhängig von der Kenntnis der Mechanismen, welche die evolutiven Veränderungen in den Populationen von Arten und den Prozess der Phylogenese steuern.“

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[1] Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004) zum Gedenken

Wir befinden uns in scharfem Gegensatz zu dieser Auffassung. Wir sind vielmehr davon überzeugt, dass es wenig befriedigend ist, ja gegen die Regeln der Naturwissenschaft verstößt, eine Abstammungshypothese nur auf dürren Apomorphien – manchmal nur einer einzigen – zu begründen, ohne diese Hypothese an der beobachtbaren Realität und den dem evolutiven Wandel zugrunde liegenden Mechanismen (= Prozessen) zu testen. Es ist unbestritten, dass man ausschließlich auf der Grundlage des vergleichend formenkundlichen Frageansatzes (der Suche nach Homologien und ihrer Wertung) die genealogischen Beziehungen der Organismengruppen untereinander rekonstruieren kann (s. o.). Heraus kommt ein formales System von Dichotomien, dessen Knotenpunkte mehr oder weniger gut durch Apomorphien gestützt sind. Die Ermittlung eines solchen Systems ist der Versuch, die Folge von Ereignissen und Änderungen zu beschreiben und in eine chronologische Ordnung zu bringen. Dabei entsteht jedoch ein Baum ohne Blüten und Blätter, ein Skelett ohne Fleisch und Blut. Kladisten, vor allem aber solche, die sich molekularer Methoden bedienen, begnügen sich allzu oft mit diesem Stand der historisch-narrativen Erklärungen (s. u.).

Phylogenien sind wissenschaftliche Erklärungen (NAGEL 1961; HEMPEL 1965, 1977; BOCK & VON WAHLERT 1963; BOCK 1981; SZALAY & BOCK 1991) eines Satzes von Beobachtungen und müssen auch als solche auf der zugrunde liegenden Theorie der organismischen Evolution beruhen und vor allem auch gegen diese getestet werden (BOCK 1981; SZALAY & BOCK 1991). Es ist selbstverständlich entscheidend für eine Phylogenie, wie die Organismen evolviert sind. Eine Phylogenie beruht vollständig auf den bekannten Mechanismen der Evolution und nicht lediglich auf der Hypothese, dass evolutiver Wandel stattgefunden hat.

Die Evolutionstheorie und die Mechanismen des evolutiven Wandels sind nomologisch-deduktive Erklärungen der organismischen Evolution (BOCK & VON WAHLERT 1963, BOCK 1981; eine ausführliche Diskussion der nomologisch-deduktiven Erklärung findet man bei NAGEL 1961 und HEMPEL 1965, 1977).

Mit der von ihm entwickelten Hypothese der Phylogenie der Gastroneuralia versucht AHLRICHS (1995) die Evolutionsgeschichte dieser Gruppen zu erklären. Da phylogenetische Hypothesen auf der Theorie der Evolution beruhen, müssen sie auch gegenüber dieser getestet werden, d.h. nomologisch-deduktive Erklärungen dienen dazu, historisch-narrative zu testen (s.u.). Damit gelangen wir zu einer *erklärenden (evolutionären) Phylogenetik*. BOCK & VON WAHLERT (1963) haben dieses Konzept der erklärenden Phylogenenetik entwickelt (siehe dazu auch OSCHE 2002). Sie unterscheiden drei Aspekte evolutionsbiologischer Untersuchungen: 1. Die reine Beschreibung von phyletischen Linien von Organismen und ihre chronologische Ordnung. Eine solche historische Studie kann man als *Phylogenetik* bezeichnen. 2. Die Untersuchung der Mechanismen des evolutiven Wandels einschließlich ihrer Ursachen und Konsequenzen. Diese Analyse der Mechanismen des evolutiven Wandels haben BOCK & VON WAHLERT (1963) als *Studium der Evolutionsprinzipien* bezeichnet. Dieser Aspekt ist, obgleich mit historischen Gegenständen befasst, keine historische Untersuchung. 3. Die möglichst vollständige, auf den Mechanismen der Evolution beruhende Erklärung der Ereignisse und des evolutiven Wandels in den phyletischen Linien der Organismen. Diesen Aspekt bezeichnen BOCK & VON WAHLERT (1963) als *erklärende (evolutionäre) Phylogenetik*. Diese ist eine historische Disziplin.

Wenn man die Entstehung neuer Gruppen, wie hier z.B. die der Gastroneuralia erklären will, dann muss man nach den Ursachen von deren Ursprung suchen; dabei müssen die bekannten Mechanismen der Evolution berücksichtigt werden. Nur wenn eine solche Erklärungsprozedur vorliegt, ist man berechtigt, eine Untersuchung *„Die Evolution der ...“* zu nennen. Wir untersuchen hier *die Evolution der Gastroneuralia.*

2. DIE EVOLUTION DER GASTRONEURALIA

2.1. Der Ursprung der Gastroneuralia

Bei der Frage nach dem Ursprung der Gastroneuralia gilt es zunächst die Frage zu beantworten: *„Woher kommen die Gastroneuralia?“* Diese Frage ist gleichbedeutend mit der Suche nach der Schwestergruppe der Gastroneuralia und der Stammart dieser beiden Schwestertaxa. Es gilt aber auch die Frage zu klären: *„Warum gibt es Gastroneuralia?“* Die Beantwortung dieser Frage ist gleichbedeutend mit dem Versuch, die Selektionswirkungen, welche die Schlüsselmerkmale der Gastroneuralia begünstigt haben, kausal zu erklären. Wir suchen also nach autapomorphen Schlüsselmerkmalen, welche die *„ökologische Zone“* (GÜNTHER 1949, 1950) der Gastroneuralia erschließen halfen. Wir müssen daher die adaptive Bedeutung folgender Merkmale begründen (funktional-adaptive Analyse nach BOCK 1981):

1. eines lediglich Millimeter großen Körperhabitus,
2. eines kurzen und dünnen, wurmförmigen und äußerlich nicht weiter untergliederten Körpers,

3. einer Lebenslaufgeschichte der Individuen, die durch eine direkte Ontogenese und frühe Geschlechtsreife gekennzeichnet ist (r-Strategie),
4. eines dorsofrontalen Cerebralganglions,
5. von mehreren Längsnervensträngen, mit einem Paar ventrolateral gelegener Hauptnervenstränge,
6. Partnerfindung und -erkennung.

Diese Merkmale sind allen ursprünglichen Gastroneuralia (Gastrotricha [Nemathelminthes], Catenulida, Gnathostomulida [Spiralia] u.a.) gemeinsame Homologien, d.h. diese Merkmale traten bei der Stammart der Gastroneuralia erstmals bei allen Individuen gemeinsam auf (Autapomorphien sensu HENNIG 1982; Abb. 1 und 2). Zu diesem Ergebnis führt die Morphologie, die ihre Erklärung aus dem formenkundlichen Vergleich gewinnt. Die Erklärungen, die durch die vergleichende Formenkunde, die Morphologie, gewonnen werden, beruhen auf dem Homologieprinzip: *„Homolog sind Strukturen, deren nicht zufällige Übereinstimmung auf gemeinsamer Information beruht"* (OSCHE 1973). In unserem Fall handelt es sich um Information, die nur von den Eltern auf die Kinder übertragen worden sein kann (das gilt in der Regel nur für genetische Information).

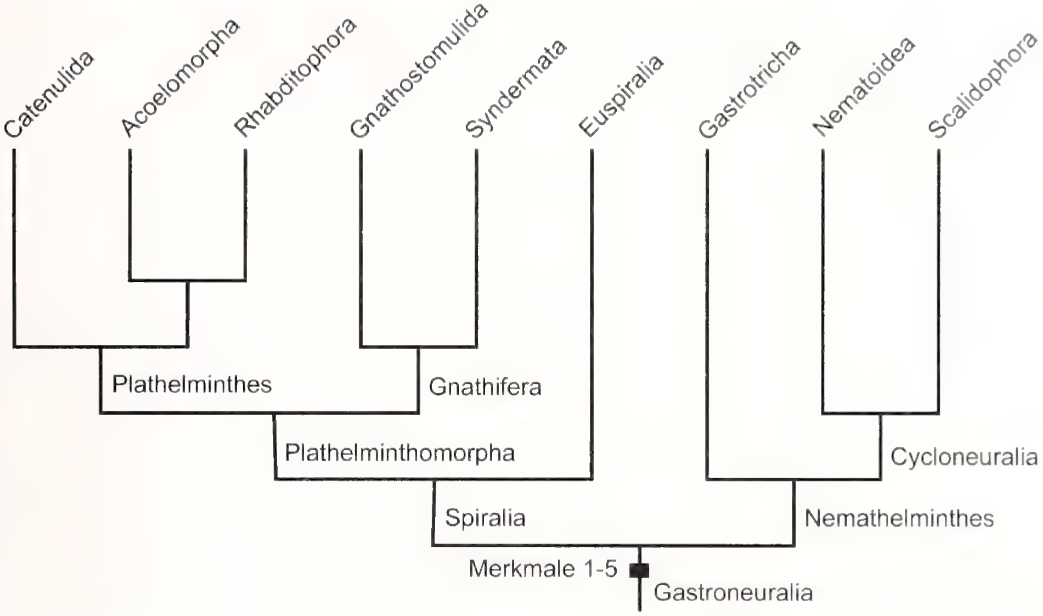

Abb. 1: Verwandtschaftsbeziehungen innerhalb der Gastroneuralia kombiniert nach AHLRICHS (1995) und EHLERS (1985).

Zur Klärung der Frage: *„Woher kommen die Gastroneuralia?"* bedienen wir uns der Regeln der vergleichenden Formenkunde. Die auf dem Homologieprinzip beruhende Morphologie führt hier zu dem partikulären Allsatz: *Alle ursprünglichen Gastroneuralia (= ursprüngliche Nemathelminthes + ursprüngliche Spiralia) sind durch die oben genannten Merkmale 1 bis 5 gekennzeichnet.* Damit gewinnt in der historischen Evolutionsforschung das Homologieprinzip eine besondere Erklärungsqualität. Das gilt hier aber lediglich für die Erklärung des historischen Ursprungs der Gastroneuralia.

Die Regeln der Morphologie entsprechen denen der deduktiven Logik und erlauben Schlussfolgerungen (Theoreme) aus Prämissen (Axiomen) hervorgehen zu lassen. Die Morphologie ist durch ihre syllogistische Schlussweise ausgezeichnet. Der Syllogismus der traditionellen aristotelischen Logik besteht aus drei Sätzen, wobei zwei die Prämissen, der dritte Satz die Konklusion bilden. In unserem Fall können wir aus den beiden Vorsätzen:

1. Wenn ein Organismus die Merkmale 1 bis 5 besitzt, ist er ein ursprünglicher Gastroneuralier,
2. Gastrotricha haben die Merkmale 1 bis 5, schließen, dass
3. Gastrotricha ursprüngliche Gastroneuralia sind.

Der Mittelbegriff „Merkmale 1 bis 5" lässt die Gastrotricha als ursprüngliche Gastroneuralia erkennen.

Die Beantwortung der Frage: *„Warum gibt es Gastroneuralia?"*, also die Suche nach den Selektionswirkungen, welche die oben genannten Schlüsselmerkmale 1 bis 5 der ursprünglichen Gastroneuralia begünstigt haben, ist lediglich durch eine historisch-narrative Erklärung (NAGEL 1961; HEMPEL 1965, 1977) zugänglich. Bevor wir dieser Erklärung nachgehen, wollen wir zunächst die Abstammungshypothese, wie sie AHLRICHS (1995) entwickelt hat, näher betrachten und ein mögliches Schwestertaxon ermitteln (Abb. 1 und 2).

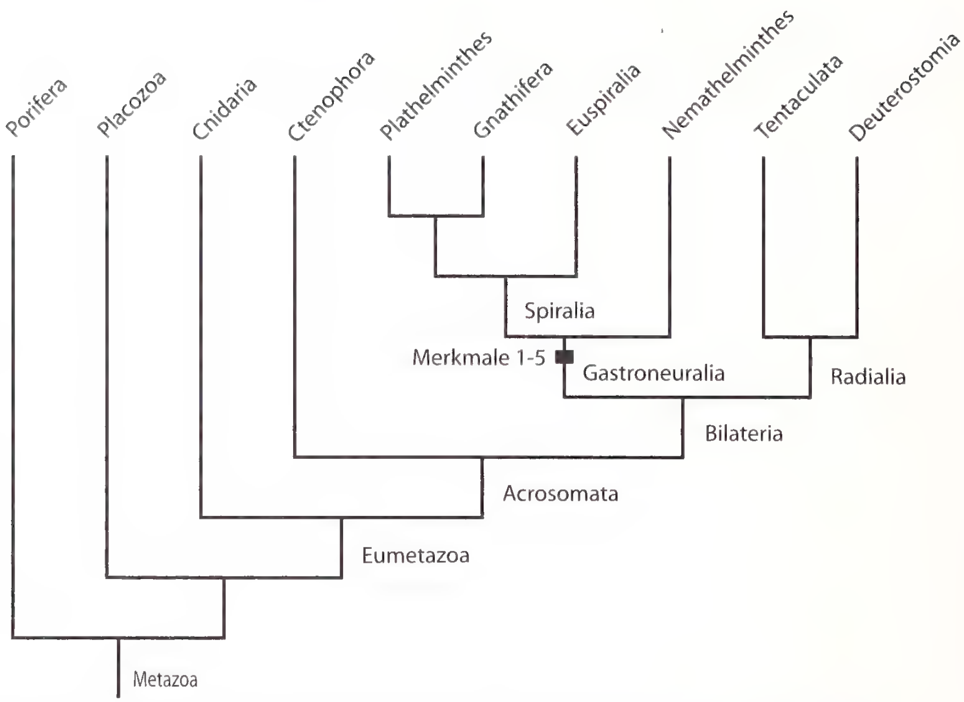

Abb. 2: Verwandtschaftsbeziehungen innerhalb der Metazoa verändert nach Ax (1995) und Ahlrichs (1995).

2.2. Die Grundmuster der Stammarten der Bilateria, Gastroneuralia und Radialia und ihre genealogischene Verknüpfung

Stellt man die Frage nach den Ursachen, die zur Evolution des Grundmusters der Gastroneuralia geführt haben, so ist es zunächst notwendig, dieses Grundmuster zu beschreiben und genau zwischen abgeleiteten Merkmalen, die in der Stammart der Gastroneuralia erstmals auftreten, und plesiomorphen Merkmalen zu unterscheiden, denn nur abgeleitete Merkmale können uns konkrete Hinweise auf die speziellen selektiven Bedingungen in der Stammlinie eines Taxon geben. Der Vergleich der grundplannahen Gruppen der Gastroneuralia liefert uns ein eindeutiges Bild: Sowohl bei den Gastrotricha (= Nemathelminthes), als auch bei den Gnathostomulida und Catenulida (= Spiralia) handelt es sich um mikroskopisch kleine Bewohner des Sandlückensystems (Mesopsammal) mit einem wurmförmigen Körper. Diese Infauna-Lebensgemeinschaft wird als Mesopsammon bezeichnet. Das Nervensystem besteht aus einem frontalen Gehirn und Längsnerven, wobei vor allem ein Paar ventrolateraler Hauptnervenstränge auffällt. Weiterhin zeigen alle basalen Gastroneuralia eine direkte Entwicklung ohne Larvenstadium.

Um zu entscheiden, ob es sich bei diesen Merkmalen um evolutive Neuerwerbungen der Gastroneuralia oder um das evolutive Erbe aus dem Grundmuster eines übergeordneten Taxon handelt, soll zunächst das Grundmuster des nächst übergeordneten Taxon, der Bilaterier, untersucht werden.

Glaubt man der überwiegenden Mehrzahl der aktuellen Lehrbücher zum Thema Spezielle Zoologie (z.B. Ax 1995), so ist die Frage nach dem Grundmuster der Bilaterier heute relativ eindeutig beantwortet. Das dort geschilderte Grundmuster gleicht bis auf ganz wenige Details dem oben geschilderten Grundmuster der Gastroneuralia. Der letzte gemeinsame Vorfahr aller Bilaterier war demnach ein kleiner, bilateralsymmetrischer, wurmförmiger Organismus, der das Benthal vorzeitlicher Meere bewohnte. Als Konsequenz seiner wurmförmigen Gestalt hatten sich ein Vorder- und ein Hinterende ausgebildet, wobei das Vorderende zum einen durch die Mundöffnung, zum anderen durch eine Konzentration von Sinnes- und Nervenzellen („Gehirn") gekennzeichnet ist. Paarige Protonephridien erlaubten dem Urbilaterier eine verbesserte Osmoregulation und somit das Leben in Medien mit wechselnder Salinität.

Eine neue Qualität erhält in der Stammlinie der Bilaterier das Mesoderm, also die Strukturen zwischen Ekto- und Entoderm (Bartolomaeus 1993). Während die Mesogloea der Cnidarier und Ctenophoren noch weitgehend aus extrazellulärer Matrix mit einzelnen, aus den angrenzenden Epithelien eingewanderten Zellen (z.B. i-Zellen = Stammzellen) besteht, findet sich bei den Bilateriern an dieser Stelle eine echte Gewebe formende Zellage, welche unter anderem für die Ausbildung eines subepidermalen Hautmuskelschlauches aus (im einfachsten Falle) einer äußeren Ring- und einer inneren Längsmuskulatur verantwortlich ist. Auch über den Lebenszyklus scheint Klarheit zu bestehen: Die Stammart der Bilaterier hatte eine direkte Entwicklung ohne pelagisches Larvenstadium.

Unklarheit über das Grundmuster der Bilaterier besteht nach diesem Szenario nur in einigen wenigen Punkten, vor allem in der Frage nach dem Vorhandensein oder Fehlen von After oder primären bzw. sekundären Leibeshöhlen.

Während sich einige dieser Merkmale bei einem Vergleich der ranghöchsten Taxa der Bilaterier tatsächlich widerspruchsfrei für die Stammart aller Bilaterier postulieren lassen, so gibt es andere Merkmale, die bei genauem Hinsehen unserer Ansicht nach einer kritischen Überprüfung bedürfen. Widerspruchsfrei sind das Vorhandensein von Protonephridien, die neue Qualität des Mesoderms als gewebebildende Zellage und die grundsätzlich bilateral angelegte Körpersymmetrie. Problematisch scheinen uns vor allem die folgenden Punkte: Der Gesamthabitus (klein, wurmförmig, im Interstitium lebend), die Cephalisation am Vorderende und das Fehlen eines pelagischen Larvenstadiums.

Der Vergleich der beiden Gruppen Radialia und Gastroneuralia (die AHLRICHS 1995 ohne Begründung als Schwestergruppen annimmt; Abb. 2) zeigt auf den ersten Blick, dass sich wurmförmige, mikroskopisch kleine Sandlückenbewohner nur innerhalb des Taxon Gastroneuralia finden lassen. Auch das Fehlen eines pelagischen Larvenstadiums finden wir nur bei den grundplannahen Gruppen der Gastroneuralia. Anders verhält es sich hingegen bei den Radialia. Phoroniden und Deuterostomia sind makroskopische, sessil oder hemisessil lebende Organismen, deren Körper keinesfalls als wurmförmig beschrieben werden kann. Vielmehr erinnern diese Gruppen in Körperbau und Lebensweise an die Polypen der Cnidarier, und wie diese ernähren sie sich filtrierend mit Hilfe eines Tentakelapparates. Weiterhin zeigen Phoroniden und Deuterostomier, wie die Cnidarier, einen pelago-benthischen Lebenszyklus (JÄGERSTEN 1972) mit einer Schwimmlarve als Propagationsstadium. Auch eine Cephalisation mit vorne liegendem Gehirn ist nicht deutlich ausgeprägt, das Nervensystem ist als diffuser Nervenplexus ausgebildet (BULLOCK & HORRIDGE 1965; SAUER & HOCH 2002). Es ist kein zwingender Grund zu erkennen, warum diese Merkmale Neuerfindungen der Radialia sein sollten.

Vielmehr scheint es uns plausibel, dass vom Grundmuster der Eumetazoa bis hin zum Grundmuster der Deuterostomia ein makroskopischer, polypenähnlicher Habitus, ein pelago-benthischer Lebenszyklus und eine mit Hilfe eines Tentakelapparates filtrierende Lebensweise kontinuierlich beibehalten wurden. Das einzige problematische Taxon bei einem solchen Szenario sind die nicht sessilen Ctenophoren (Abb. 2). Zwar sind auch sie makroskopisch, auch sie ernähren sich mit Hilfe von Tentakeln und auch ihr Habitus lässt sich, analog der Meduse der Cnidarier, von einem polypenähnlichen Typ ableiten, allerdings besitzen sie eine direkte Entwicklung ohne Larve. Ihre von dem „normalen" radiären Furchungstyp der Cnidaria und Radialia abweichende biradiale Furchung lässt jedoch vermuten, dass die Entwicklung der Ctenophoren ein abgeleitetes Eigenmerkmal der Ctenophoren darstellt und unserer Argumentation somit nicht im Wege steht.

Durch das hier dargestellte Szenario erhält auch eine alte und von vielen für überholt angesehene Überlegung in leicht abgewandelter Form neue Aktualität. Im Laufe der Anagenese der Radialia könnten die Coelome, so wie bereits in der Archicoelomaten-Theorie (MASTERMAN 1898; REMANE 1950; JÄGERSTEN 1955; SIEWING 1969, 1980) vorgeschlagen, aus einer Trennung der hydrostatischen und der verdauenden Funktion des Gastrovaskularsystems, also aus Gastraltaschen hervorgegangen sein, wie sie bei Cnidariern ausgebildet sind und auch für die Stammart der Eumetazoa hypothetisiert werden. Die Bildung der Coelome aus Entodermzellen bei den Tentaculaten und aus Darmabfaltungen bei Deuterostomiern kann als Indiz hierfür gewertet werden. Anders verhält es sich bei den Coelomen der Euspiralier. Dass ihre Coelome nicht homolog zu den Coelomen innerhalb der Radialer sind, ist weitgehend anerkannt (z.B. BARTOLOMAEUS 1993). Vielmehr entstehen innerhalb der Euspiralia, vermutlich unabhängig, Coelome als Eigenbildungen der Taxa Nemertini, Mollusca und Articulata. Für ein Vorhandensein oder den Verlust von Coelomen im Grundmuster der Gastroneuralia gibt es keinerlei Hinweise.

Folgt man den hier ausgeführten Überlegungen, stellt sich das Grundmuster der Bilaterier wie folgt dar: Der Urbilaterier war ein makroskopisch großer, polypenähnlicher Organismus, der sich mit Hilfe eines Tentakelkranzes, auf Sedimentböden siedelnd, filtrierend ernährte. Das bedeutet, es hat in der Stammlinie der Bilateria ein *Lebensortwechsel* vom Hartsubstrat, wo die ursprünglichen Eumetazoa siedelten, auf Sedimentböden stattgefunden. Das Nervensystem ist diffus organisiert (BULLOCK & HORRIDGE 1965; SAUER & HOCH 2002) und der Lebenszyklus beinhaltet ein pelagisches Larvenstadium. Autapomorphien der Bilaterier sind eine bilateral angelegte Körpersymmetrie, Protonephridien und ein Gewebe bildendes Mesoderm, welches u.a. für die Ausbildung eines Hautmuskelschlauches verantwortlich ist. Dieses Grundmuster wird von den Deuterostomiern mit einigen wenigen Abwandlungen, vor allem der Ausbildung von Coelomen, übernommen.

Starke evolutive Veränderungen finden hingegen in der Stammlinie der Gastroneuralia statt. Ihre auffälligste Autapomorphie ist ein mikroskopisch kleiner, wurmförmiger Habitus, verbunden mit einen Wechsel des Lebensortes in das Sandlückensystem. Als Folge dieser Veränderungen ist es weiterhin zur Cephalisation und der Ausbildung von Längsnerven gekommen. Die Ursachen und der Verlauf der Evolutionsgeschichte der Bilateria, Gastroneuralia und Radialia sowie deren genealogische Verknüpfung können nur historisch-narrativ erklärt werden.

3. DIE HISTORISCH-NARRATIVE ERKLÄRUNG

3.1. Charakterisierung des Erklärungstyps

Zur Erklärung von Phänomenen des Lebendigen müssen in der Evolutionsbiologie *historische Faktoren* berücksichtigt werden. Aus diesem Grund treffen wir in dieser Disziplin auf den historisch-narrativen, den entwicklungsgeschichtlichen Frageansatz (NAGEL 1961; HEMPEL 1965, 1977). Jede phänotypische Gestalt, aber auch jede Form von ökologischer Interaktion der Individuen mit ihrer Umwelt ist das augenblickliche Endprodukt eines einmaligen historischen Prozesses. Die diesem Prozess zugrunde liegende Kausalität entzieht sich der unmittelbaren experimentellen Prüfung. Aus diesem Grund ist in diesem Zusammenhang eine andere als die nomologisch-deduktive Erklärungsprozedur erforderlich, nämlich die historisch-narrative. Dieses Erklärungsverfahren beschreibt ein zu erklärendes Merkmal, also auch jeden Typ von ökologischer Interaktion, als letztes Ergebnis einer einmaligen Entwicklungsfolge. Damit wird das betrachtete Phänomen durch Erzählen der aufeinander folgenden Entwicklungsstadien erklärt. Ziel einer historisch-narrativen Erklärung ist es, nachzuweisen, wie *„ein Zustand zum nächsten führt“* (HEMPEL 1965, 1977), wie also aufeinanderfolgende Zustände (Merkmalsausprägungen) *durch allgemeine Gesetzmäßigkeiten miteinander verknüpft sind.* Damit wird z.B. die Evolution eines jüngeren Zustands einigermaßen wahrscheinlich gemacht. Im Falle der Beantwortung der Frage: *„Warum gibt es Gastroneuralia?“* gilt es, die Selektionswirkungen zu rekonstruieren, welche die Entstehung der oben genannten Merkmale 1 bis 5 begünstigt haben. Historisch-narrative Erklärungen beinhalten also einerseits einen gewissen Anteil nomologischer Verknüpfungen, andererseits aber auch einen Anteil an Beschreibung. Dieses von NAGEL (1961) und HEMPEL (1965, 1977) entwickelte Erklärungsverfahren hat einerseits Ähnlichkeit mit dem nomologisch-deduktiven Verfahren und andererseits mit dem rein beschreibenden Verfahren. In der Praxis wird man diese beiden Verfahren nicht strikt trennen können. Auch wird man die aufeinander folgenden Zustände einer Entwicklungsfolge nicht vollständig auflösen können. Daher wird eine historisch-narrative Erklärung eine Vielzahl von Tatsachen und Ereignissen beschreiben, die sich über einen bestimmten Zeitraum verteilen.

Wir wollen hier prüfen, ob die Evolution der abgeleiteten Grundmustermerkmale der Gastroneuralia einer historisch-narrativen Erklärung zugänglich sind. Ist dies der Fall, dann gewinnt die phylogenetische Hypothese von AHLRICHS (1995) an Wahrscheinlichkeit. Um diese phylogenetische Hypothese zu testen, unterziehen wir die Schlüsselmerkmale der Gastroneuralia einer funktional-adaptiven Analyse (BOCK 1981).

3.2. Die funktional-adaptive Analyse der Schlüsselmerkmale der Gastroneuralia

Die Evolutionstheorie und die Mechanismen des evolutiven Wandels (z.B. Änderungen von Anpassungen) sind nomologisch-deduktive Erklärungen. Eine Phylogenie ist dagegen ein Versuch, die evolutionäre Geschichte einer bestimmten Gruppe – hier die der Gastroneuralia – zu rekonstruieren. Jedes dabei genutzte Merkmal ist das augenblickliche Endprodukt eines einmaligen historischen Prozesses. Die diesem Prozess zugrunde liegende Kausalität entzieht sich, wie bereits festgestellt, der unmittelbaren experimentellen Prüfung. Aus diesem Grund muss die Erklärungsprozedur von den Evolutionsmechanismen zur Phylogenie fortschreiten, d.h. nomologisch-deduktive Erklärungen können zum Testen historisch-narrativer Erklärungen herangezogen werden, niemals aber umgekehrt (BOCK 1981).

Im folgenden werden wir die Randbedingungen untersuchen, die zur *Kleinheit, direkten Entwicklung und frühen Geschlechtsreife* (Merkmale 1 bis 3) der Stammart der Gastroneuralia geführt haben. Dazu müssen wir die Umweltprobleme kennen, welche die Stammart der Gastroneuralia zu lösen hatte. Wir müssen versuchen, den ursprünglichen Lebensort und die ursprüngliche Lebensweise der Gastroneuralia zu rekonstruieren.

3.3. Rekonstruktion des ursprünglichen Lebensortes der Gastroneuralia

Zur Rekonstruktion des ursprünglichen Lebensortes der Stammart der Gastroneuralia müssen wir uns den rezenten Lebensort der Individuen der ursprünglichen Gruppen der Gastroneuralia näher ansehen. Die ursprünglichen Gruppen der Gastroneuralia sind die Gastrotricha, Catenulida, Gnathostomulida u.a. (siehe Abb. 1). Die Individuen der Arten dieser Gruppe sind lediglich 0,1 bis 1 mm lang und leben überwiegend in Sedimenten mit limitierter Sauerstoffverfügbarkeit. Die zu lösenden Umweltprobleme der Individuen dieser interstitiellen Fauna – der Meiofauna – gehen von der Korngröße der Partikel der Sedimente, vor allem aber von der limitierten *Sauerstoffverfügbarkeit* aus.

In den Sedimenten entwickeln sich anoxische Zonen. FENCHEL & RIEDL (1970) nannten diese anoxischen Zonen und die sie besiedelnden Organismen das „Sulfid-Biom". Dieses „Sulfid-Biom" wird vor allem durch die ursprünglichen Gastroneuralia gebildet. BOADEN & PLATT (1971) haben diese Lebensgemeinschaft das „Thiobios" genannt, ein Begriff, der allgemein angenommen worden zu sein scheint.

Wir haben hier nicht den Raum, um auf die umfangreiche Diskussion über die ursprüngliche Anaerobiose verschiedener Meiofauna-Arten bzw. der Metazoa überhaupt einzugehen (z.B. BRYANT 1991; FENCHEL & FINLAY 1995). Wir stimmen jedoch mit REISE & AX (1979) überein und weisen die Hypothesen, dass die Metazoen während des Präkambriums in anoxoischer Umwelt evolviert sein sollen, bzw. dass sich unter den ursprünglichen Gastroneuralia primär anaerobe Meiofauna-Arten befinden, entschieden zurück. Dieses Problem berührt unsere Überlegungen auch in keiner Weise (siehe unten).

Das sogenannte „Sulfid-Biom" hat eine scharfe Obergrenze, wo das Redox-Potential mit der Sedimenttiefe rapide von positiven zu negativen Werten übergeht. Diese Grenze wird als Redox Diskontinuitäts-Zone (RDZ) bezeichnet. Unterhalb dieser Grenze werden die Bedingungen anoxisch. Wenn das Redox-Potential negative Werte annimmt, so geht man davon aus, dass im allgemeinen kein O_2 mehr vorhanden ist. Im sauerstoffarmen Bereich dieser Zone leben allerdings zahlreiche Vertreter der ursprünglichen Gastroneuralia (FENCHEL & RIEDL 1970; HUMMON 1972; LASSERRE & RENAUD-MORNANT 1973; OTT & SCHIEMER 1973, WIESER et al, 1974; BOADEN 1975, 1977; HOGUE 1978; BOADEN & ELHAG 1984).

Ein solch harscher Lebensraum stellt seine Bewohner vor schwierige ökologische Probleme, vor allem durch die limitierte O_2-Verfügbarkeit. *Welches ist das präadaptive Plateau, das die Nutzung dieses an organischer Substanz und an „ungenutzten" Ressourcen reichen, jedoch starken Sauerstoffschwankungen unterworfenen Lebensraumes möglich gemacht hat?* Wie mag eine erbliche phänotypische Varianz in der Effizienz der Nutzung von O_2 bei geringem O_2-Partialdruck [pO_2] entstanden sein?

Um diese Fragen zu beantworten, müssen wir die Ausbildung und Entwicklung der Atmosphäre der Erde genauer ansehen (KASTING et al. 1992). Die Zunahme des O_2-Partialdrucks der Atmosphäre der Erde wurde in den letzten 50 Jahren intensiv diskutiert (NICHOLAS 1991, FENCHEL & FINLAY 1995). Bei welchem pO_2 in der Genese der Atmosphäre der Erde haben sich eine aerobe Biochemie und erste aerobe Organismen eingestellt? Unter welchem pO_2 sind die Stammarten der Metazoa, Eumetazoa, Bilateria, Gastroneuralia und Radialia entstanden? Die rezente O_2-Konzentration beträgt 1 PAL O_2 = 20.9 % ≅ 0.2 Atm [PAL 0_2 present atmosphere O_2-level]. Vor 1.5 Milliarden Jahren hatte sich eine O_2-Konzentration von 0.01 PAL O_2 = 0.2 % ≅ 2 x 10^{-3} Atm. eingestellt. Dieser pO_2-Wert entspricht dem sogenannten *Pasteur-Punkt,* das ist die O_2-Konzentration, bei der amphiaerobe Organismen von aeroben auf anaeroben Stoffwechsel umschalten. Vor 1 Milliarde Jahren betrug der pO_2-Wert etwa 0.1 PAL O_2 ≅ 2 % (KASTING et al. 1992).

Es ist nicht unrealistisch, die Evolution der Bilateria vor einer Milliarde Jahren anzusetzen (BENTON & AYALA 2003). *Damit hat die noch früher anzusetzende Evolution der frühen Metazoa wie die der Bilateria bei geringerer O_2-Verfügbarkeit stattgefunden.*

Diese geringe O_2-Verfügbarkeit ist ein Umweltproblem, auf das es verschiedene organismische (adaptive) Antworten gibt. „Ziel" eines aeroben Organismus muss es sein, den limitiert verfügbaren Sauerstoff an die Erfolgsorgane zu bringen. Dieses „Ziel" kann grundsätzlich auf mehreren Wegen erreicht werden: 1. dadurch, dass die Diffusionsstrecke des Sauerstoffs durch dünne, einschichtige Epithelien, die allseits von sauerstoffhaltigem Meerwasser umgeben sind, so gering wie möglich gehalten wird (z.B. bei den Cnidaria, die auch in ihrem Gastrovaskularsystem Meerwasser enthalten; Abb. 2), 2. durch Kleinheit des Organismus (z.B. ursprüngliche Gastroneuralia; Abb. 1) oder 3. durch die Entwicklung eines O_2-Transportsystems, eines Kreislaufsystems, bei größeren Bilateria mit deutlich entwickeltem Haut-Muskel-Schlauch (z.B. bei den Phoronida, den altertümlichsten rezenten Radialia; Abb. 2). Den Zusammenhang zwischen pO_2, Respiration durch Diffusion des O_2 durch Gewebe und die Größen- bzw. Gewebsdickebegrenzung bei Organismen können wir quantifizieren und nomologisch-deduktiv erklären. Dazu bedienen wir uns einer Formel, die HILL (1929) entwickelt hat, welche den Radius eines Zylinders bestimmt, der O_2-Diffusion bis in das Zentrum erlaubt. In unserer Betrachtung setzen wir dabei voraus, dass ein möglicher zylinderförmiger Organismus, wie z.B. ein ursprünglicher Gastroneuralier a) eine konstante Stoffwechselrate besitzt und b) der pO_2 konstant ist. Diese Formel lautet

$$r_o = \frac{4k \times y_o}{a}$$

wobei

r_o = Radius

k = Diffusionskoeffizient von O_2 ins Gewebe (n. ATKINSON 8.4 x 10^{-4} cm^2/atm/h)

y_o = O_2-Partialdruck (atm)

a = Stoffwechselrate in cm^3 O_2/cm^3 Gewebe/h (konst.)

Die Stoffwechselrate ist aber ihrerseits größenabhängig. Diese Beziehung folgt nach NICHOLAS (1984, 1991) folgender Formel

$$\frac{Y}{X} = a(b-1)$$

Y = O_2-Verbrauch
X = Gewicht
a und b = Konstanten

ATKINSON (1976, 1980) nutzte publizierte O_2-Verbrauchswerte (Y) von freilebenden Nematoden und setzte b = 0.79 um die Rate a des O_2-Verbrauchs in Abhängigkeit von der Körpergröße zu bestimmen. Diese Betrachtung führt zu dem Ergebnis, dass ein Meiobenthos-Organismus mit einem Radius von 25 µm etwa 0.6 nl 0_2/mg Feuchtgewicht/h nutzt (NICHOLAS 1984, 1991). Das wiederum bedeutet, dass die aerobe Respiration eines Organismus mit einem Radius von 50 µm oder weniger solange nicht O_2-limitiert ist, wie der O_2-Partialdruck 15 mm Hg (= 10% = 0.1 PALO_2) der atmosphärischen Luft nicht unterschreitet (vor 0.5 bis 1.0 Milliarden Jahren; NICHOLAS 1991).

Durch unvorhersagbare O_2-Schwankungen war der Lebensort der ursprünglichen Gastroneuralia sehr instabil. Das führte dazu, dass es in den Populationen der diesen Lebensort bewohnenden Arten zu *dichteunabhängigen* und *unvorhersagbaren* Mortalitätsepisoden kam. Das hatte einen tiefgreifenden Einfluss auf die Lebenslaufgeschichte der Individuen der Arten, die einen solchen Lebensort nutzten. Solche unvorhersagbaren und dichteunabhängigen Mortalitätsepisoden führen zu r-selektierten Merkmalsgefügen (PIANKA 1970; SOUTHWOOD 1980): kleine, kurzlebige Organismen mit früher Geschlechtsreife und schneller Entwicklung sowie kurzer Generationszeit. Sogenannte r-Selektion ist dann zu erwarten, wenn starke, regelmäßige, aber unvorhersagbare Umweltschwankungen regelmäßige Mortalitätsereignisse nach sich ziehen, aber gleichzeitig mit einer hohen Nahrungsverfügbarkeit verknüpft sind (PIANKA 1970; SOUTHWOOD 1980). Solche Umweltbedingungen begünstigen eine hohe Fekundität, frühe Geschlechtsreife und schnelle Entwicklung eines kleinen Organismus. Mit der r-Selektion ist auch *Progenese* verbunden (GOULD 1977). *Progenese* ist die in der Ontogenese zeitlich vorverlegte Reproduktion.

In den Populationen der Stammlinien der Acrosomata, Bilateria und Gastroneuralia (Abb. 2) muss eine erbliche phänotypische Variabilität in bezug auf den *pelago-benthischen Lebenszyklus* (JÄGERSTEN 1972) der Individuen der Populationen dieser Stammlinien existiert haben. Zunächst muss es eine erbliche phänotypische Variabilität der *Habitat-Selektion* der Larven der Individuen der Populationen der Stammlinie der Acrosomata gegeben haben. Während die Individuen der Populationen der Stammlinie der Ctenophora zu einem *rein pelagischen Lebenszyklus* übergegangen sind, haben die Individuen der Populationen der Stammlinie der Bilateria und Radialia (Abb. 2) den ursprünglichen pelago-benthischen Lebenszyklus beibehalten, was man daran erkennen kann, dass die Phoroniden als ursprüngliche Radialia einen pelago-benthischen Lebenszyklus mit einem sessilen Adultus und einer der Propagation dienenden mobilen Larve haben. Die Individuen der Populationen der Stammlinie der Gastroneuralia sind dagegen zu *einem rein benthischen Lebenszyklus* übergegangen.

Der Übergang zu einem rein benthischen Lebenszyklus mit direkter Entwicklung muß durch eine erbliche phänotypische Variabilität zwischen den Individuen der Populationen der Stammlinie der Gastroneuralia in bezug auf den lebenslaufgeschichtlichen Zeitpunkt der Geschlechtsreife und Reproduktion möglich geworden sein. In diesen Populationen – so hypothetisieren wir – gab es in bezug auf die Lebenslaufgeschichte zwei Phänotypen: zum einen Individuen, die während ihrer Lebenslaufgeschichte zweimal geschlechtsreif wurden, einmal in der Juvenilphase und dann noch einmal als sogenannte Adulti; dieses Phänomen der Dissogonie ist z.B. von Ctenophora bekannt. Der zweite Phänotyp wurde durch Progenese (GOULD 1977) nur noch einmal in einem frühen Ontogenesestadium geschlechtsreif. Diese Individuen der Populationen der Stammlinie der Gastroneuralia, die sich unter den r-selektierenden Randbedingungen schließlich nur noch einmal zu einem sehr frühen Ontogenesezeitpunkt reproduziert haben, müssen gegenüber den Individuen mit Dissogonie den nicht zufällig höheren Reproduktionserfolg gehabt haben, also selektionsbegünstigt gewesen sein.

In diesem Zusammenhang ist es wichtig zu berücksichtigen, dass alle Arten der ursprünglichen Gastroneuralia durch eine *direkte Entwicklung* ausgezeichnet sind. Wenn Larven bei den Gastroneuralia auftreten (z.B. die Müllersche oder die Goettesche Larve bei den Polycladida), so sind diese nicht den primären Larven aus dem pelago-benthischen Lebenszyklus der Metazoa, Eumetazoa, Bilateria und Radialia homolog, sondern sind sekundäre Larven (JÄGERSTEN 1972). Vielmehr spricht einiges dafür, dass die Larven des primär pelago-benthischen Ontogeneseverlaufs in der Stammlinie der Gastroneuralia geschlechtsreif geworden sind (Progenese) und damit gewissermaßen ein neuer, sich direkt ohne Larve entwickelter Adultus entstanden ist.

Die Synthese all dieser beobachtbaren Evidenz sowie der hinzugefügten, für die Erklärung der Evolution der Gastroneuralia wichtigen Überlegungen, erlaubt den Schluss, dass die geringe Größe, direkte Entwicklung und der ontogenetisch frühe Fortpflanzungszeitpunkt der ursprünglichen Gastroneuralia ursächlich durch die gravierenden pO_2-Schwankungen in den an nutzbarer organischer Substanz reichen Sedimenten durch r-Selektion erzwungen wurde. Die Evolution der Gastroneuralia ist demnach mit einem Wechsel im Lebensort und in der Lebensweise verbunden.

3.4. Lebensort- und Lebensweisewechsel in der Evolution der Gastroneuralia

Um die Evolutionsgeschichte von Art-Taxa zu verstehen und zu erklären, muss man ihre Ökologie untersuchen, die das Ergebnis der wirksamen Evolutionsprozesse ist: Während des historischen Ablaufs, den man „Makroevolution“ nennt, d.h. im Verlauf von Anagenese (adaptiver phyletischer Wandel) und Cladogenese (adaptive Radiation) evolvieren vollständig neue Umweltbezüge, neue ökologische Nischen. Nach GÜNTHER (1949, 1950), HUTCHINSON (1957, 1959) und BOCK (1979) versteht man unter der ökologischen Nische einer Art zwei Dimensionssysteme, die organismischen (autozoischen) Dimensionen, die in einem definierten biotischen und abiotischen Umweltausschnitt (dieser bildet die ökischen Dimensionen) „eine Rolle spielen“. Der Deckungsbereich beider Dimensionssysteme wird von GÜNTHER (1950) als ökologische Nische definiert. Die Güte der Passung der Individuen der Populationen einer Art in die für sie spezifischen Umweltbedingungen, ihre Adaptiertheit (Adaptivness), entscheidet über ihre Fitness. Während intraspezifische Konkurrenz zur Nischenerweiterung führen kann, verursacht interspezifische Konkurrenz Nischendifferenzierung. Die Bildung einer Nische setzt 1. ungenutzte, in der Regel nur begrenzt verfügbare Ressourcen als *„ökologische Lizenzen“* (GÜNTHER 1950) und 2. Merkmale als *„organismische Lizenzen“* (OSCHE 1983) voraus, welche die Nutzung der ökologischen Lizenzen ermöglichen. Dabei spielen bereits vorhandene, in einem alten Umweltbezug entstandene Anpassungen, Praeadaptationen, eine Rolle, die in dem neuen Nischenbezug eingesetzt werden, was zu neuen Selektionsszenarien führt. Dabei sind vielfach Verhaltensänderungen „Schrittmacher der Evolution“ (MAYR 1970). Während der Anagenese und Cladogenese bilden „Schrittmacherarten“ „Schlüsselmerkmale“ (organismische Strukturen) aus, die einen Wechsel im Umweltbezug herbeiführen können. Durch einen solchen Wechsel im Umweltbezug können ökologische Nischen entstehen, die wir *ex post faktum* als neue *ökologische Zonen* (GÜNTHER 1950; SIMPSON 1953) erkennen können. Ökologische Zonen erlauben die adaptive Radiation der „Schrittmacherart“. Dabei wird die ökologische Zone in zahlreiche ökologische Nischen „aufgeteilt“. Diesen Vorgang nennt man kurz gesagt Makroevolution; das ist 1. der Ursprung und die langfristig umfassende Änderung von Anpassungen und damit verbunden die Entstehung neuer, gegenüber den alten bemerkenswert unterschiedlicher Umweltbezüge sowie 2. den Ursprung und die adaptive Radiation eines Taxon von höherem kategorialem Rang.

Der historische Übergang vom Grundmuster der Eumetazoa zu dem der Bilateria und schließlich zum Grundmuster der Gastroneuralia ist eine solche makroevolutionäre Ereigniskette. Während dieses Prozesses, der vollständig auf die Mechanismen reduziert werden kann, die für mikroevolutive Veränderungen ursächlich sind (RENSCH 1972), kommt es oft zu einem tiefgreifenden *Lebensort-* und *Lebensweisewechsel.*

Lebensort-Typen umfassen nach RIEDL (1966) „Repräsentanten geschlossener (und aus Anpassungsreihen gleichen Ursprungs hervorgehender) Verwandtschaftsgruppen, welche jeweils weitgehend einheitlich und zumeist nur mehr historisch zu verstehende Bindungen der Gruppenmerkmale an das gemeinsame Biotop aufweisen“. Der ursprüngliche Lebensort der Eumetazoa ist das Hartsubstrat im Litoral urzeitlicher Meere. Durch eine Verhaltensänderung der Larve im pelago-benthischen Lebenszyklus der Individuen der Populationen in der Stammlinie der Bilateria hat spätestens seit der Evolution der Schrittmacherart der Bilateria ein Lebensortwechsel stattgefunden. Die Larven dieser Schrittmacherart änderten ihre Habitat-Selektion und siedelten auf Weichböden, die durch eine hohe Verfügbarkeit ungenutzter Ressourcen, aber auch durch eine geringe O_2-Verfügbarkeit (s.o.) ausgezeichnet waren und sind. Der Lebensort der Phoroniden und die Habitat-Selektion der Actinotrocha-Larve (HERRMANN 1976, 1979) sind dafür Indizien. Während in der Stammlinie der Radialia der Lebensort-Typ beibehalten wurde, ist in den Populationen der Stammlinie der Gastroneuralia ein weiterer neuer Lebensort-Typ entstanden, der *im* Sediment lebende Urgastroneuralier, der durch die Merkmale 1 bis 5 gekennzeichnet war.

Mit dem Lebensortwechsel vom Hart- auf den Weichboden war zunächst kein Lebensweisewechsel verbunden. Der Urbilaterier muss ein sessiler Filtrierer von makroskopischer Dimension (RIEGER et al. 1991) und polypenähnlichem Habitus gewesen sein. Ob schon bei diesem Urbilaterier die Trennung der hydrostatischen Funktion (Coelom) von der verdauenden Funktion (Darm) des Gastrovaskularsystems der Eumetazoa vorgelegen hat, wie es bei den Radialia der Fall ist, bleibt offen. Vielleicht können wir einmal dem *„Ignorabimus“* ein mutiges „wir werden wissen“ entgegensetzen.

In der Stammlinie der Gastroneuralia hat der Lebensortwechsel des Urgastroneuraliers auch zu einem Lebensweisewechsel geführt. Wieder müssen wir davon ausgehen, dass eine Verhaltensänderung die Schrittmacherfunktion bei der Erschließung des ursprünglichen Lebensortes der Gastroneuralier hatte. Die Larven im noch pelago-benthischen Lebenszyklus der Individuen der Populationen der Stammlinie der Gastroneuralia besiedelten das Interstitial mariner Weichböden, wo – wie oben bereits dargestellt – diese Larven durch den Prozess der Progenese zu frühreifen, frei beweglichen Adulti (GOULD 1977) wurden. Die Adaptation an geringe O_2-Verfügbarkeit sowie an dichteunabhängige und unverhersagbare Mortalitätsepisoden reichte jedoch noch nicht aus, um diesen „unwirtlichen", aber ungenutzten Lebensraum zu nutzen. Die Schlüsselart der Gastroneuralia muss die mikrophage Lebensweise ihrer progenen Larve als Adultus beibehalten haben. Dafür spricht, dass alle ursprünglichen Gastroneuralia mikrophag sind; z.B. ernähren sich die Catenulida von Bakterien, Flagellaten und Diatomeen (KAESTNER 1964, S. 230) und die Gastrotricha von Bakterien, Flagellaten, Foraminiferen und Diatomeen (KAESTNER 1964, S. 272). Da wir auch bei den Planulae der Anthozoa, den grundplanähnlichsten Eumetazoa, eine Mundöffnung kennen, dürfen wir annehmen, dass auch die Larve der Stammart der Eumetazoa eine solche hatte. Bei diesem Typ Planula-Larve handelt es sich grundsätzlich um eine Gastrula mit Gastralraum, deren Blastoporus während der Metamorphose als Mundöffnung persistiert (SIEWING 1969). Diese planktotrophen Larven sind durch ein funktionstüchtiges entoblastemales Epithel ausgezeichnet; mit Hilfe der Cilien des Peristoms strudeln diese Larven Nano- und Mikroplankton in ihre Mundöffnung (NYHOLM 1943). Damit ist naheliegend, dass die Schlüsselart der Gastroneuralia an die mikrophage Lebensweise präadaptiert war.

Zur Lebensweise gehört auch der Fortpflanzungsmodus. Der Fortpflanzungsmodus der Cnidarier, Ctenophoren, Phoroniden, Echinodermen und Ascidien ist die *äußere Besamung.* Das spricht sehr stark dafür, dass die Individuen der Populationen der Stammlinie der Eumetazoa-Bilateria-Radialia-Deuterostomia-Chordata durch den ursprünglichen Fortpflanzungsmodus der *äußeren Besamung* gekennzeichnet waren. Der Begriff äußere Besamung beschreibt im hier besprochenen Zusammenhang die ungezielte Abgabe von Keimzellen ins freie Wasser. Dabei findet die Syngamie sozusagen „fernab" der Elterntiere statt. Organismen mit solchermaßen äußerer Besamung sind gezwungen, die Verbindung zum freien Wasserkörper zu erhalten. Mit dem Fortpflanzungsmodus der äußeren Besamung ist daher ein Lebensortwechsel, wie er in der Stammlinie der Gastroneuralia stattgefunden hat, nicht zu vollziehen. Es ist leicht einzusehen, dass die ungezielte Abgabe von Eizellen und Spermien in die Umgebung bei Bewohnern des Interstitials aufgrund stark reduzierter Begegnungswahrscheinlichkeit der Keimzellen den Reproduktionserfolg von Individuen mit äußerer Besamung an diesem Lebensort stark mindern würde. Um den Lebensortwechsel in das Interstitial mariner Weichböden vollziehen zu können, mussten die Individuen der Populationen der Stammlinie der Gastroneuralia zunächst einen an diesen Lebensort angepassten Fortpflanzungsmodus entwickeln.

3.5. Lebensort-Typ und Fortpflanzungsmodus

Unter den Randbedingungen des von den ursprünglichen Gastroneuralia genutzten Lebensortes sind solche Individuen selektionsbegünstigt, die ihre Spermien möglichst nahe an die Eier des Paarungspartners heranbringen. Die anagenetisch „vollkommenste" Lösung dieses Problems ist die auf eine Kopulation folgende *innere Besamung.* Dieser Begriff der *inneren Besamung* beschreibt jedoch keinen einheitlichen, im Tierreich homologen Merkmalskomplex. Vielmehr ist der Komplex *„Kopulation mit nachfolgender innerer Fertilisation"* bei den Metazoa vielfach unabhängig entwickelt worden. Und so kann der Merkmalskomplex *„innere Besamung"* auch keine Autapomorphie der Gastroneuralia sein. Während die ursprünglichen Gruppen der Euspiralia noch den ursprünglichen Fortpflanzungsmodus der äußeren Besamung aufweisen, sind die ursprünglichen Gruppen der Nemathelminthes und Spiralia (sensu AHLRICHS 1975; Abb. 1) durch eine innere bzw. quasi innere Besamung ausgezeichnet.

Der anagenetische Schritt zur inneren Besamung macht eine Kopulation der Geschlechtspartner notwendig. Eine „echte" Kopulation, d.h. eine Vereinigung der Genitalarmaturen und nachfolgende Injektion von Spermien in den weiblichen Genitalsitus wurde aber erst möglich, nachdem bereits komplizierte Partnerfindungs-, Partnererkennungs- und Paarungsmechanismen entwickelt worden waren. Die Merkmalskomplexe Partnerfindung und -erkennung sind mögliche Autapomorphien der Gastroneuralia. Die Validität dieser Hypothese gilt es in Zukunft zu prüfen.

Die innere Besamung wird bei den ursprünglichen Vertretern der Gastroneuralia, nachdem die Individuen der Populationen der Stammlinie Partnerfindungs- und -erkennungsmechanismen entwickelt hatten, auf konvergentem Wege durch „parallele evolutive Vervollkommnung" (REGENFUSS 1975) erreicht. Die Art und Weise, wie bei den Macrodasyiden, ursprünglichen Gastrotrichen (REMANE 1936), die Spermien übertragen werden, ist sehr vielfältig. Das spricht für die konvergente Entwicklung der inneren Besamung auch in dieser Gruppe. Betrachten wir ein Beispiel etwas näher. Bei dem protantrischen Zwitter (die ursprünglichen Gastroneuralia haben den Hermaphroditismus aus der Stammlinie Metazoa-Eumetazoa-Bilateria beibehalten; SAUER 1996) *Dactylopodola baltica* wird zunächst bei einem männlich gestimmten Individuum an der rechten Körperseite eine Ausstülpung, die Spermatophore, gebildet, in welche die Spermien einwandern. Diese Spermatophore wird auf ein Individuum, welches sich in der weiblichen Phase befindet, übertragen (TEUCHERT 1968). Hat ein männlich gestimmtes Individuum dieser Art ein weiblich gestimmtes gefunden und erkannt, dann heftet es die Spermatophore genau an der Stelle an, wo das weiblich gestimmte Individuum in seiner männlichen Phase seine Spermien gebildet hatte. Die Spermien dringen dann an dieser Stelle in den Körper ein und wandern zu den Eiern (TEUCHERT 1968).

Für unsere Überlegungen ist die Tatsache, dass bei Gastrotrichen die Eier nach der Fertilisation durch Ruptur der Körperwand abgegeben werden (TEUCHERT 1968) besonders interessant. Das erinnert an den Modus der Abgabe von Keimzellen bei Cnidaria und Ctenophora. Dieser Befund spricht sehr stark dafür, dass die Gastrotrichen neben der Entwicklung neuer auch ursprüngliche Merkmale des Fortpflanzungsverhaltens aus den Grundmustern der Eumetazoa-Bilateria beibehalten haben. Auch bei den Catenuliden werden die Eier nach der Besamung durch Ruptur der Körperwand entlassen (KARLING 1974; EHLERS 1985), d.h. auch die ursprünglichen Spiralia haben – wie die ursprünglichen Nemathelminthen – alte Merkmale des Fortpflanzungsverhaltens aus den Grundmustern der Eumetazoa-Bilateria beibehalten. Bei den ursprünglichen Nemathelminthes und Spiralia umhüllen keine speziellen Wandzellen die Keimlager (HENDELBERG 1983; EHLERS 1985), was an das Grundmuster der Eumetazoa erinnert. Sowohl innerhalb der Nemathelminthen, vor allem aber bei den Spiraliern, wird die innere Besamung, verbunden mit immer komplexer werdenden Genitalsitus, erreicht.

Den ursprünglichen Gastroneuralia muss es trotz der Beibehaltung ursprünglicher Merkmale des Fortpflanzungsverhaltens aus dem Grundmuster der Eumetazoa schon sehr früh auf verschiedenen Wegen gelungen sein, die innere Besamung zu erreichen. Das bedeutet, dass die Individuen der Populationen der Stammlinie der Gastroneuralia schon sehr früh Partnerfindungs- und Partnererkennungsmechanismen entwickelt haben müssen. Das ermöglichte ihnen eine *„quasi innere"* Besamung ihrer Eier; sie gaben ihre Keimzellen wahrscheinlich in unmittelbarem Körperkontakt ins freie Wasser ab. Dieses Verhalten könnte die Praeadaptation zur Nutzung des Interstitials mariner Weichböden, dem Lebensort der ursprünglichen Gastroneuralia, gewesen sein.

Die Evolution der Merkmale 4 und 5 der ursprünglichen Gastroneuralia (Abb. 2), das gegenüber den Cnidariern und Phoroniden viel komplexere Nervensystem, steht wahrscheinlich mit dem Erwerb von Partnerfindungs- und Partnererkennungsmechanismen in ursächlichem Zusammenhang. Solche Mechanismen setzen eine entsprechende Sensorik und neurale Informationsverarbeitung voraus.

3.6. Konsequenzen der Änderung des Fortpflanzungsmodus der Gastroneuralia für ihre adaptive Radiation

Innere Fertilisation erlaubt auch Spermienspeicherung und macht wiederholte Paarungen möglich, ehe die ersten Eier besamt und abgelegt werden. Das führt zwangsläufig zur Konkurrenz der Spermien verschiedener Spermienerzeuger um die begrenzt verfügbaren und besambaren Eier (PARKER 1970), was wiederum Wirkungen der *sexuellen Komponente der Selektion* verursacht.

Bevor wir auf die bis heute stark unterschätzte Bedeutung der sexuellen Komponente der Selektion für die Steigerung der Geschwindigkeit der ökologisch-adaptiven Differenzierung (SAUER 1996) während der adaptiven Radiation einer Gruppe zu sprechen kommen, müssen wir kurz auf die Verknüpfung der Inhalte der Konzepte Selektion, natürliche Selektion und sexuelle Selektion eingehen. Generell ist Selektion nicht zufällig differentielle Zygotenbildung bzw. Reproduktion verschiedener Individuen einer Population. Dabei bezieht sich der Ausdruck *„nicht zufällig"* auf die selektionsverursachende phänotypische Varianz und ihre Heritabilität. FISHERS (1930) *fundamentales Theorem der Selektion* besagt, dass die Änderungsrate eines Merkmals zu jeder Zeit der diesem Merkmal zugrunde liegenden additiven genetischen Varianz proportional ist. Worin liegt der heuristische Wert einer weiteren Differenzierung der generellen Wirkung der Selektion in eine *natürliche* und eine *sexuelle Wirkungskomponente*? DARWIN (1859) hat das Konzept der natürlichen Selektion entwickelt, um mechanistisch zu erklären, wie sich Merkmale in Populationen über Generationen hinweg graduell verändern. Dabei hat er nicht immer strikt zwischen Überlebens- und Fortpflanzungserfolg unterschieden. Ihm war jedoch als erstem klar geworden, dass die unterschiedliche erbliche phänotypische Ausprägung von Merkmalen ihre Träger zu unterschiedlich guter Auseinandersetzung mit ihrer Umwelt befähigt (Kampf ums Dasein), was letztlich dazu führt, dass in einer Population „besser" angepasste Phänotypen häufiger, „schlechter" angepasste hingegen seltener wurden. Dieses Ergebnis unterschiedlichen individuellen Erfolgs hat DARWIN (1859) *„natürliche Auslese"* genannt. Das Konzept der *„sexuellen Selektion"* hat DARWIN (1859, 1871) entwickelt, da gewisse Besonderheiten in der Fortpflanzungsbiologie der Tiere sich einer mechanistischen Erklärung durch sein Konzept der *natürlichen Selektion* (1859) entzogen. Mit dem *Konzept der sexuellen Selektion* suchte DARWIN (1859, 1871) dem Dilemma zu entkommen, dass die meist männlichen Träger von extravaganten Strukturen durch die Wirkung der natürlichen Selektion Erfolgsminderungen zu erwarten haben. Einen Ausweg sah Darwin darin, dass die Träger solcher extravaganten Merkmale, wie z.B. das Schwanzgefieder des Pfaus, durch eine höhere Attraktivität für die Weibchen einen höheren Fortpflanzungserfolg erzielen sollten, um dadurch wiederum den durch die Wirkung der natürlichen Selektion erzwungenen Nachteil zu kompensieren (DARWIN 1872, S. 64): „Diese Form der Selektion wird nicht durch den Kampf ums Dasein in bezug auf andere Lebewesen oder äußere Bedingungen verursacht, sondern durch die Fortpflanzungskonkurrenz zwischen den Individuen des einen Geschlechts, im allgemeinen des männlichen, um den Besitz des anderen Geschlechtes" (übersetzt von den Verfassern). Diese nicht zufällig differentielle Konkurrenzüberlegenheit beim Partnergewinn hat DARWIN (1871, 1872) *„sexuelle Selektion"* genannt.

Die Theorie der Lebenslaufgeschichte besagt, dass sich Individuen zu jedem Zeitpunkt ihres Lebenslaufes so verhalten müssen, dass sie am Ende eine maximal mögliche Zahl von Nachkommen erzielen. Auf diesem Weg müssen die Individuen verschiedene ökologische Probleme lösen, d.h. Selektionsfilter passieren. Alle biotischen und abiotischen Widerstände der Umwelt, welche *nicht zufällig differentielles Überleben und/oder nicht zufällig differentiellen Ressourcengewinn* bewirken, sind Faktoren, welche natürliche Selektion verursachen. Haben die Individuen schließlich den Reproduktionszeitpunkt erreicht, wird durch *nicht zufällig differentiellen Paarungspartnergewinn* die sexuelle Komponente der Selektion wirksam. Die nicht zufällig differentielle Reproduktion bzw. Zygotenbildung (Selektion) ergibt sich also aus dem nicht zufällig differentiellen Überleben und dem nicht zufällig differentiellen Ressourcengewinn, der in Reproduktion investiert werden kann (natürliche Komponente der Selektion) und dem nicht zufällig differentiellen Partnergewinn (sexuelle Komponente der Selektion).

Unter dem hier behandelten Gesichtspunkt der kausalen Erklärung von phylogenetischen Mustern und der ihnen zugrunde liegenden Mechanismen der ökologischen Differenzierung ist von besonderem Interesse, dass LANDE (1982) die Möglichkeit untersucht hat, ob entlang von Merkmalsklinen Artbildung durch die Wirkung der sexuellen Komponente der Selektion möglich ist. Er zeigte, dass es durch den Fisher-Prozess grundsätzlich möglich ist, dass sich parapatrische Populationen in verschiedene Richtungen entwickeln und dadurch starke Unterschiede in *Geschlechtspartner-Erkennungssystemen* herausbilden, die schließlich zu neuen Arten führen können.

Im Zusammenhang mit der ökologischen Differenzierung einer Art während des Prozesses der Radiation ist das Indikator-Modell (ZAHAVI 1975; MAYNARD-SMITH 1991; IWASA et al. 1991) der sexuellen Selektion besonders wichtig. Modelle dieses Mechanismus gehen davon aus, dass die „Pracht" der extravaganten Merkmale mit der Güte der Angepasstheit ihrer Träger korreliert. Die Weibchen erkennen also am sexuellen Signal (Indikator) die genetisch-ökologische Qualität ihres potentiellen Partners. Dadurch wird der Einfluss des Zufalls bei der Vereinigung der väterlichen und mütterlichen Gene, der bei äußerer Besamung extrem hoch ist, sehr stark reduziert. Durch die Wirkung der sexuellen Komponente der Selektion wird die ökologisch-adaptive Differenzierung von Arten stark beschleunigt (SAUER 1996).

Artengruppen, deren Mitglieder starker sexueller Selektion unterliegen, sind in der Regel artenreicher, also ökologisch stärker differenziert, als solche, deren Mitglieder im wesentlichen der natürlichen Komponente der Selektion unterliegen (SAUER 1996). Während von den Nemathelminthen (sensu AHLRICHS 1995) etwa 17.000 Arten bekannt sind, kennen wir von den Spiraliern (ohne Arthropoden) ca. 160.000 Arten. Die Arthropoden mit komplizierten Partnerwahlmechanismen haben alleine über zwei Millionen Arten hervorgebracht. Von den „Tentaculata" und Echinodermata, zwei subordinierten ursprünglichen Taxa der Radialia, sind insgesamt lediglich 12.000 Arten bekannt.

Dieser grobe Vergleich der Artenzahlen macht den Zusammenhang deutlich, der zwischen der ökologischen Differenzierung (Artenzahl) eines Taxon und dem Ausmaß der in den Populationen seiner Mitgliedsarten wirksamen sexuellen Komponente der Selektion besteht (SAUER 1996).

Arten, die starker sexueller Selektion unterliegen, sollten weniger gefährdet sein, auszusterben. Für diese Hypothese haben wir einen indirekten Hinweis. Die Mitglieder der basalen Gruppen der Radialia haben alle eine äußere Besamung. Die Wirksamkeit der sexuellen Komponente der Selektion ist also in diesen Gruppen äußerst gering. Die „Fremdheit", mit der die Gruppen der „Tentaculata", Echinodermata, „Hemichordata" und Tunicata nebeneinander stehen, lässt eine genealogische Verbindung nur schwer erkennen und macht wahrscheinlich, dass von der adaptiven Radiation der basalen Radialia nur artenarme Restgruppen überlebt haben. Die Mehrzahl muss ausgestorben sein. Leider gibt es dazu keinen Hinweis im Fossilbericht. Diese beobachtbare Realität unterstreicht erneut die Notwendigkeit einer *erklärenden (evolutiven) Phylogenetik,* d. h. die Berücksichtigung der wirksamen Mechanismen bei der historisch-narrativen Erklärung der Phylogenie einer Gruppe.

4. EPILOG

Die funktional-adaptive Analyse (BOCK 1981) der Merkmale, durch welche die ursprünglichen Vertreter der Gastroneuralia (= Nemathelminthes + Spiralia, sensu AHLRICHS 1995) ausgezeichnet sind (Merkmale 1 bis 5; Abb. 1), legt nahe, die Nemathelminthes und Spiralia auf eine gemeinsame Stammlinie zurückzuführen, wie es AHLRICHS (1995) mit seinem *Gastroneuralia-Konzept* vorgeschlagen hat.

Durch die Synthese der beobachtbaren Tatsachen und der erzählend hinzugefügten, für die Beantwortung der Frage *„Warum gibt es Gastroneuralia?"* wichtigen Befunde und Überlegungen, ist es nicht gelungen, das Gastroneuraliakonzept von AHLRICHS (1995) zu falsifizieren. Allerdings muss hier ausdrücklich angemerkt werden, dass die Hypothese von AHLRICHS (1995), die Schlüsselart der Gastroneuralia hätte ihren millimetergroßen, kurzen, wurmförmigen und äußerlich nicht weiter untergliederten Körperhabitus aus dem Grundmuster der Bilateria übernommen, entschieden zurückgewiesen werden muss. Diese Auffassung AHLRICHS (1995) ist durch die mehrheitlich vertretene und akzeptierte Auffassung belastet, der Urbilaterier sei ein Organismus von millimetergroßem Habitus und direkter Entwicklung (Zusammenstellung der relevanten Literatur siehe bei RIEGER et al. 1991). Wir teilen hier vielmehr die Auffassung von RIEGER et al. (1991), dass die Stammart der Bilateria ein Organismus mit pelago-benthischem Lebenszyklus und einer acoelomaten, kurzlebigen Larve von mikroskopischer Dimension gewesen sein muss. Aus einer solchen Larve mit Mundöffnung und Gastralraum (SIEWING 1969; NYHOLM 1943) entwickelte sich in der Ontogenese ein (vielleicht coelomater, s.o.) sessiler Filtrierer von makroskopischer Dimension (cm-Bereich).

Die Frage *„Warum gibt es Gastroneuralia?"* beantworten wir auf folgende Weise: Die mikroskopische Körpergröße, die direkte Entwicklung sowie die ontogenetisch frühe Geschlechtsreife und der damit verbundene ontogenetisch frühe Fortpflanzungszeitpunkt des Urgastroneuraliers wurde durch einen Lebensortwechsel der Larve eines ursprünglich noch pelago-benthischen Lebenszyklus in eine r-selektierende Umwelt erzwungen. Dem Lebensortwechsel ging also eine Verhaltensänderung, die Habitat-Selektion der Larve betreffend, voraus. Mit dem Habitatwechsel in das Sediment gelangte die Larve in einen an ungenutzten Ressourcen reichen Lebensort. Das r-selektierende Umweltszenario an diesem Lebensort wurde von unvorhersagbaren pO_2-Schwankungen und damit verbundenen unvorhersagbaren und dichteunabhängigen Mortalitätsepisoden bestimmt. Dieser Lebensortwechsel des Urgastroneuraliers in das Sediment mariner Weichböden, wo äußere Besamung (der ursprüngliche Fortpflanzungsmodus der Bilateria) aufgrund der reduzierten Begegnungswahrscheinlichkeit der Keimzellen selektionsbenachteiligt sein muss, war den Individuen der Populationen der Stammlinie der Gastroneuralier nur durch den Erwerb von Partnerfindungs- und Partnererkennungsmechanismen möglich geworden. Diesen Merkmalskomplex der Partnerfindung hypothetisieren wir als Schlüsselmerkmal (Autapomorphie) der Gastroneuralia.

Dieser Merkmalskomplex der Partnerfindung war das präadaptive Plateau (OSCHE 1962), von dem aus die Individuen der Populationen der Stammlinie der Gastroneuralia durch Ablaichen auf kleinstem Raum zunächst zur *„quasi internen"* Besamung ihrer Eier gelangten. Das änderte das Selektionsszenario. Durch parallele Vervollkommnung wurde dann in den verschiedenen Gruppen die *„innere Besamung"* durch die Entwicklung der unterschiedlichsten Genitalsitus erreicht. Die Evolution eines dorsofrontalen Cerebralganglions, verbunden mit mehreren Längsnervensträngen, von denen zwei ventrolateral gelegene besonders auffallen (Merkmale 4 und 5), dürfte in ursächlichem Zusammenhang mit der umfangreiche Informationsverarbeitung notwendig machenden Partnerfindung und -erkennung stehen. Partnerfindung und -erkennung sowie „quasi innere" bzw. „innere" Besamung waren zwingende Voraussetzungen zur Bildung der *ökologischen Zone der Gastroneuralia.*

Danksagung. Herrn Prof. Dr. Dr. h. c. Günther Osche, Freiburg, danken wir für die kritische Durchsicht des Manuskriptes und für zahlreiche wertvolle Hinweise. Frau Monika Schmied sind wir für ihre sorgfältige Reinschrift des Manuskriptes zu besonderem Dank verpflichtet.

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Bonner zoologische Beiträge | Band 53 (2004) | Heft 1/2 | Seiten 165–167 | Bonn, Juni 2005

Peridea clasnaumanni spec. nov. (Lepidoptera: Notodontidae) aus China[1]

Alexander SCHINTLMEISTER, Dresden (Germany)

Abstract. *Peridea clasnaumanni* is described as a new species from southeast China. It represents the southern sister-species of *P. aliena* (Staudinger, 1892).

Zusammenfassung. *Peridea clasnaumanni* wird als für die Wissenschaft neue Art aus Südost-China beschrieben. Es handelt sich um die südliche nächstverwandte Art von *P. aliena* (Staudinger, 1892).

BESCHREIBUNG

Holotype: ♂, China, NE. Jiangxi, Wuyi Shan, 1600m, 50km SE Yingtan, 27°56'N, 117°25'E, April 2002, leg. V. Sinjaev and native collectors in coll. A. Schintlmeister, Dresden.

Paratypen: (13 ♂♂ 2 ♀♀):

7 ♂♂,1 ♀, NE. Jiangxi, Wuyi Shan, 1600 m, 50 km SE Yingtan, 27°56'N, 117°25'E, Mai 2002; 2 ♂♂, ibid, Juni 2002, 4 ♂♂, Jiangxi, Wuyi Shan, Xipaihe, 27°54'N, 117° 20'E, Juli 2003, 1500 m (GU 79-98); 1 ♀, Hunan, Cili, 3.ix.1988; (alle in coll. A. Schintlmeister, Dresden, ein ♂ in coll. Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn - ZFMK)

Diagnose. Vorderflügellänge (rechter Vorderflügel von Basis bis zum Apex gemessen) ♂♂ 26-30 mm, im Mittel 28.5 mm, ♀♀ 34 mm. Die neue Art ähnelt habituell *P. aliena* (Staudinger, 1892), beschrieben aus dem Amurgebiet und *P. hoenei* Kiriakoff, 1963, beschrieben aus Yunnan. Sie ist deutlich kleiner als *P. aliena* (Vorderflügellänge im Mittel ca. 23 mm bis maximal 25 mm bei den ♂♂ und 27 mm bei den ♀♀).

Die Antennen der ♂♂ bei *P. clasnaumanni* kurz gekämmt, bei den ♀♀ filiform. Thorax schwarzbraun, Abdomen rötlichbraun gefärbt. Die Vorderflügel schwarzbraun mit kontrastierender, orangebrauner Zeichnung. Auffallend ist das postbasale schwarz verdunkelte, von orangebraunen Binden eingefaßte Mittelfeld, daß im Gegensatz zu *P. aliena* und insbesondere zu *P. hoenei* die Costa der Vorderflügel nicht erreicht. Ein gutes Erkennungsmerkmal ist ferner der orangebraune, hellbraun eingefaßte und auffallende Discoidalfleck. Die Vorderflügel zeigen weiterhin eine undeutliche, auf den Hinterflügeln fortgesetzte Postmedianbinde sowie eine gleichartige Submarginalbinde, die sich ebenfalls auf den Hinterflügeln fortsetzt. Die Hinterflügel sind schwarzgrau und deutlich dunkler gefärbt als *P. aliena* oder *P. honei*. Charakteristisch sind die oben erwähnten Postmedian- und Submarginalbinden der Hinterflügel, die zum Außenrand zu hell abgesetzt sind.

Der Sexualdimorphismus ist habituell gering entwickelt.

Die männlichen Genitalien sind denen von *P. aliena* ähnlich. Der Uncus von *P. clasnaumanni* ist weniger stark eingebuchtet und weniger ausladend, die Socci sind im Vergleich zu *P. aliena* dicker und auch zugespitzt. Die Valve ist hat keinen, wie bei *P. aliena* abgesetzten Apex, der dorsale Valvenfortsatz in Nähe des Apex ist dicker und es fehlen die für *P. aliena* charakteristischen zwei kleineren Fortsätze in Nähe der Basis der Valve. Der Aedoeagus ist sehr charakteristisch durch den hakenförmigen Fortsatz (größer als bei *P. aliena*) und ein ausgedehntes (größer als bei *P.aliena*) Gebiet mit zahlreichen Cornuti; *P. hoenei* hat, wie viele andere Arten der Gattung *Peridea* keine Cornuti.

Der 8. Sternit mit dem für die Arten der Gattung typischen Anhängen, jedoch der Mittelteil nicht eingebuchtet wie etwa bei *P. aliena*.

Verbreitung. Die Typenserie von *P. clasnaumanni* wurde in Südost-China gefunden (Provinzen Jiangxi, Hunan). Aus SW Yunnan, Xishuangbanna, 60 km N Jinghong, 1000 m liegen mir zwei Männchen vor, die zur neuen Art gehören, jedoch deutlich heller gezeichnet sind. Möglicherweise handelt es sich um eine eigene Unterart, weshalb diese beiden Exemplare nicht in die Typenserie aufgenommen werden.

Nächste Verwandte. *P. clasnaumanni* ist vor allem wegen der äußerst ähnlichen Genitalstrukturen (Aedoeagus, Uncus, Socii) offenbar die Schwesterart von *P. aliena*.

Etymologie. Dem Andenken von Clas NAUMANN gewidmet.

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[1] Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004) zum Gedenken

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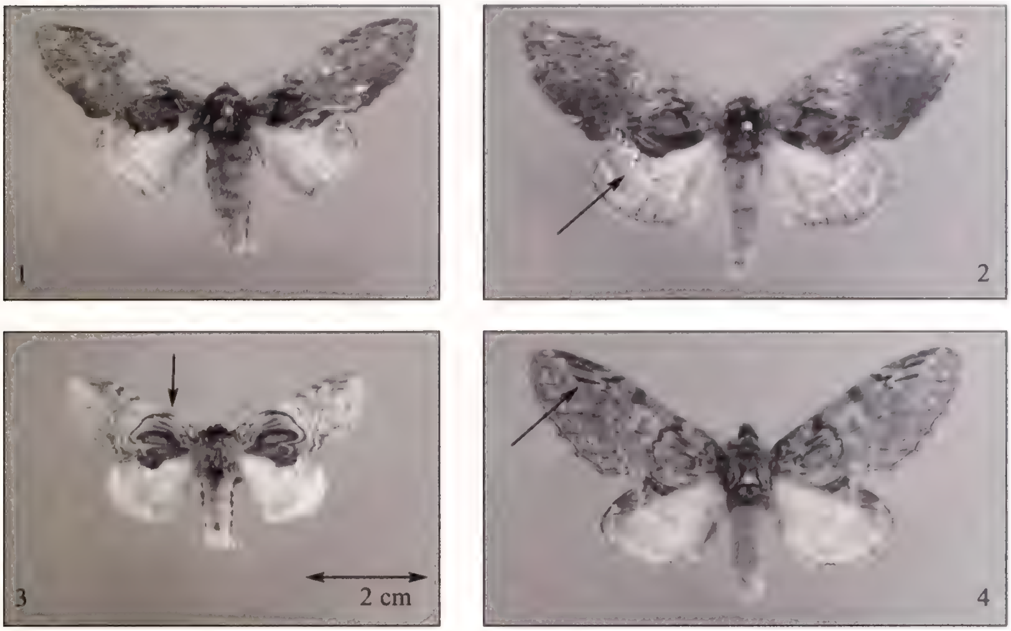

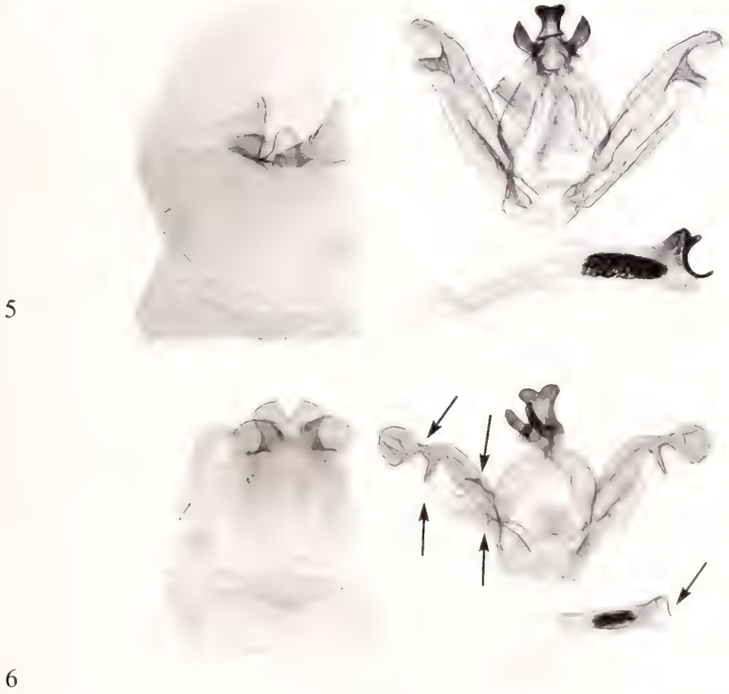

Abb. 1-4: Imagines *Peridea*. (1) *Peridea clasnaumanni* – ♂, China, NE. Jiangxi, Wuyi Shan, 1600 m, 50 km SE Yingtan, 27°56'N, 117°25'E, April 2002, Holotype. (2) *Peridea clasnaumanni* – ♀, China, Hunan, Cili, 3.ix.1988, Paratype. (3) *Peridea aliena* – ♂, Russia, Primorye, 30 km NE Wladiwostok, 24.vii.1963. (4) *Peridea hoenei* – ♀, China, Sichuan, Daxue Shan, 40 km W Mianning, 2750 m, 7.-8.vii.1998.

Abb. 5-6: Genitalapparate *Peridea*. (5) *Peridea clasnaumanni* – ♂, China, Jiangxi, Wuyi Shan, Xipaihe, 27°54'N, 117° 20'E, July 2003, 1500 m (GU 79-98), Paratype. (6) *Peridea aliena* – ♂, N. Korea, Myohang san, Myohang-Shon-valley, 24.-30.vi.1985 (GU 24-73).

Bonner zoologische Beiträge | Band 53 (2004) | Heft 1/2 | Seiten 169–185 | Bonn, Juni 2005

The Variance of Variation: Geographic Patterns of Coat Colouration in *Anomalurops* and *Anomalurus* (Mammalia, Rodentia, Anomaluridae)[1]

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Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany

Abstract. Variation of coat colouration in *Anomalurops beecrofti*, *Anomalurus derbianus*, *A. pelii*, and *A. pusillus* was studied. Character states of the dorsal and ventral colouration were defined for each species and specimens assigned to classes accordingly. Geographic patterns were analysed after excluding sex, age, and collection month as possible causes for different colouration. Considerable differences were found among the first three species, while no differences in colouration were found in *A. pusillus*. *Anomalurops beecrofti* varies in the distribution area mainly in the frequencies of different colour morphs, while in *Anomalurus derbianus* several character states are clearly restricted to defined areas. In *A. pelii* the correlation between colouration and locality is very strong, although its distribution area is much smaller than in the other species. Geographic barriers, especially rivers, are discussed as possible causes for the observed variation.

Key words. Scaly-tailed flying squirrels, morphology, colouration, Africa, biogeography.

1. INTRODUCTION[1]

The history of the African rain forest has attracted the interest of numerous researchers for a long time (e.g. BR→STRUP 1935; FJELDSÅ & LOVETT 1997; GRUBB 1978, 1990; HAMILTON & TAYLOR 1991; LÖNNBERG 1929). Besides more or less direct methods like the analysis of fossil pollen records (e.g. BRENAC 1988; FREDOUX & TASTET 1988; LIVINGSTONE 1966; MALEY 1983, 1991), the recent distribution of species and subspecies of animals was used to reconstruct this history. The anomalurid species investigated here are all able to perform a gliding flight and depend on the occurrence of large trees as starting and landing points. They are strictly arboreal and behave clumsily on the ground, and therefore their current distribution patterns may reveal information on the history of their habitat, the African rain forest.

Considerable differences are found in the variation of coat colouration in the species of Anomaluridae. *Anomalurus pusillus* Thomas, 1887, *Idiurus macrotis* Miller, 1898, *I. zenkeri* Matschie, 1894 and *Zenkerella insignis* Matschie, 1898 show a more or less uniform colouration throughout their distribution range. *Anomalurops beecrofti* (Fraser, 1853) varies in the amount of golden brown colour on the back and reddish colour on the ventral side. The most pronounced colour variation is found in *Anomalurus derbianus* (Gray, 1842), with a range from more or less uniformly brownish individuals to colourful individuals with several defined markings. *Anomalurus pelii* (Schlegel & Müller, 1845) shows only black and white in a specific pattern, but the relative portions of these colours vary.

This study describes the variation of the coat colouration in one species of *Anomalurops* and in three species of *Anomalurus* on the basis of 966 museum specimens. This sample represents the majority of skins of these species kept in research collections worldwide and is regarded as a reliable basis for a study of geographic variation.

2. MATERIAL AND METHODS

2.1. Data basis

Specimens used for this analysis were studied in 15 collections of the following institutes: American Museum of Natural History (AMNH, New York), The Natural History Museum (BMNH, London), Field Museum of Natural History (FMNH, Chicago), Liverpool Museum (LIVCM, Liverpool), Museum National d'Histoire Naturelle (MNHN, Paris), Musée Royal d'Afrique Centrale (MRAC, Tervuren), Naturhistorisches Museum Basel (NHMB, Basel), Naturhistorisches Museum Wien (NMW), Naturhistoriska Riksmuseet (NRM, Stockholm), Naturalis/Nationaal Natuurhistorisch Museum (RMNH, Leiden), Naturmuseum Senckenberg (SMF, Frankfurt/Main), National Museum of Natural History (USNM, Washington), Zoologisches Forschungsinstitut und Museum Alexander Koenig (ZFMK, Bonn), Zoölogisch Museum Amsterdam (ZMA), and Museum für Naturkunde (ZMB, Berlin). The colour and colour patterns were analysed from colour slides taken together with a colour reference. Photographs were taken of the dorsal side of all specimens and as many as possible (depending on the preparation) of the ventral side of *A.*

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[1] In commemoration of Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004)

beecrofti and of several specimens of *A. derbianus* and *A. pelii*. Sex was either determined from the skins or labels, from which also the date of collection was recorded. The relative age was estimated from tooth wear if the skull was available (details to be published elsewhere). In addition, slides were taken of 128 specimens of *A. pusillus* and compared but not used in the final analysis because it was not possible to define any differences in colouration. The data basis for the analyses is given in Table 1. The maps given in Figures 3 to 5 are based exclusively on skins with coordinates of the collection locality.

2.2. Statistics

Relationships between the various colouration characters and sex, age, and month of collection were checked with chi-square tests performed in SPSS 10.0. In the reported results the number of specimens used for the and *P* values are given (n.s. = not significant). Additionally, the percentage of cells with an expected frequency less than five (CEF<5) is given when it is higher than 0 analysis (n), the statistic (χ^2), degrees of freedom (d.f.) and the minimum expected frequency (MEF) if it is less than 1. The same test was performed to check for statistically significant differences between geographically neighbouring populations.

3. COLOURATION CODING AND RESULTS

3.1. *Anomalurops beecrofti*

The most frequent colouration of *A. beecrofti* is a silvery-grey on the back with a central stripe of golden brown from the neck over the larger part of the back. The ventral side is basically greyish or yellowish with an orange throat and chest.

Colour variation in *A. beecrofti* can be defined by the extent of the golden brown stripe on the back and the amount of orange colour on the ventral side (Plate I).

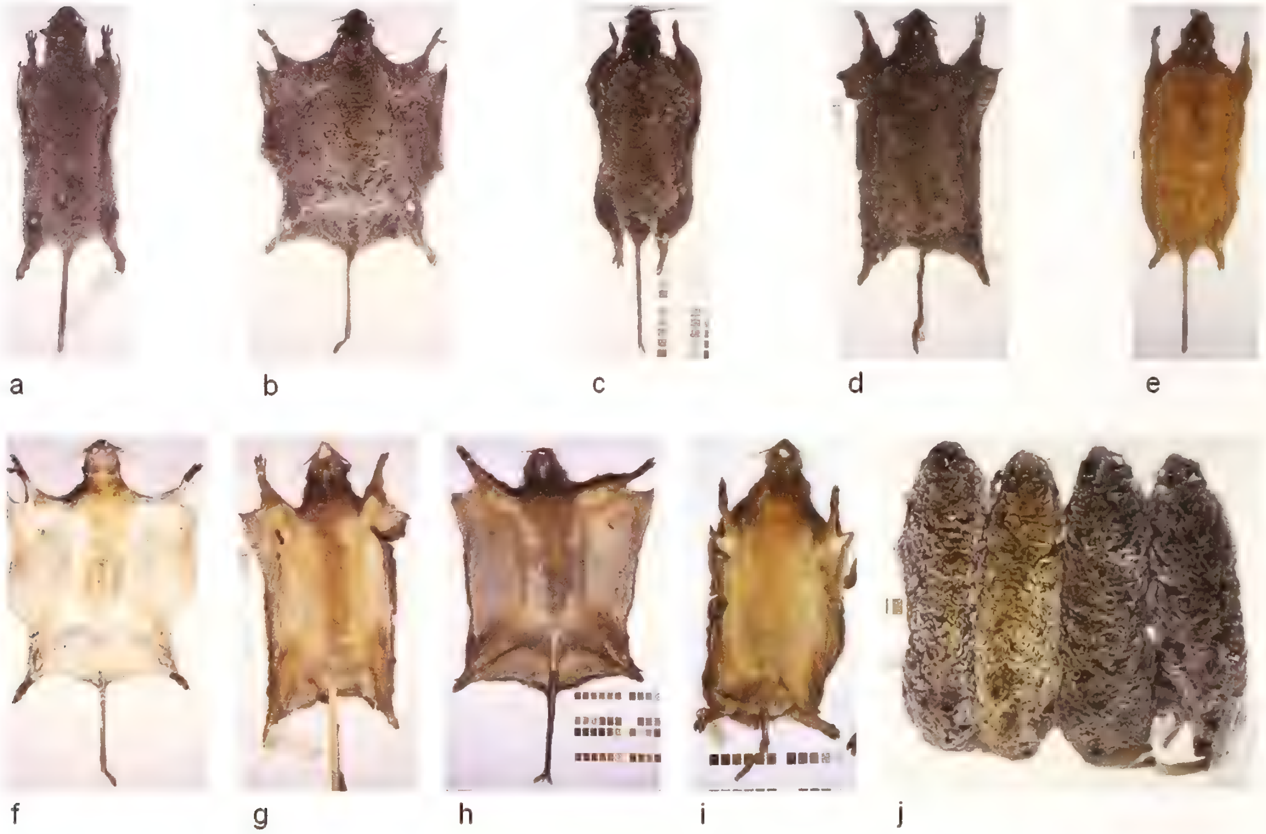

Plate I: Typical representatives of the dorsal and ventral colouration classes in *Anomalurops beecrofti* (see text for details). a: dorsal colouration DC 1 (AMNH 86845), b: DC 2 (BMNH 67.1461), c: DC 3 (USNM 84547), d: DC 4 (BMNH 96.10.9.10), e: DC 5 (BMNH 0.2.5.14), f: ventral colouration VC 1 (BMNH 67.1461), g: VC 2 (BMNH 96.10.9.10), h: VC 3 (ZFMK 64.501), i: VC 4 (MRAC 3234), j: four specimens from the same collection with (from left) DC 2 (NMW B1319), DC 4 (NMW B1325), DC 3 (NMW B1326), DC 2 (NMW B1336).

Colouration codes and frequencies

Dorsal colouration (DC):

1. back completely silvery grey without golden brown parts (4%, n=9).
2. back silvery grey, golden brown central stripe not wider than head (43%, n=98).
3. central stripe wider than head, but at least patagia silvery grey (28%, n=63).
4. back completely golden brown, central part can be slightly darker than patagia (23%, n=52).
5. back and patagia uniformly reddish orange (2%, n=5).

Ventral colouration (VC):

1. light grey or yellowish with or without light yellow central stripe (22%, n=38).
2. light grey or yellowish with orange central stripe (42%, n=71).
3. light orange and/or dark grey with orange central stripe (21%, n=36).
4. uniformly orange (14%, n=24).

Five specimens with the very peculiar dorsal colouration 5 (uniformly reddish orange) were omitted from the analysis because they strongly increased the percentage of cells with expected frequencies less than five and decreased the minimum expected frequency for the chi-square tests.

Dorsal and ventral colouration

When the four specimens with colouration 5 are omitted from the analysis, the percentage of CEF<5 is 25% and the MEF is 1.07. The result shows a strong association between dorsal and ventral colouration (χ^2 22.419, d.f. 9, p<0.01).

The interpretation of the uniformly reddish specimens is difficult for two reasons; first because of the very peculiar colour which does not fit into the other definitions of the dorsal colouration and secondly because of the very small number of specimens (5). Thus results from this group have to be treated with caution.

For the other colouration classes the correlation between dorsal and ventral colouration can be best described by differences in the frequencies. Although almost all possible combinations of dorsal and ventral colourations occur, it is obvious that individuals with larger golden brown parts on the back are likely to have also darker and more orange underparts (Fig. 1). The percentage of the two lighter ventral colouration forms decreases regularly from 88% in dorsal colouration (DC) 1 to 79% and 58% in DC 2 and 3 to 41% in DC 4.

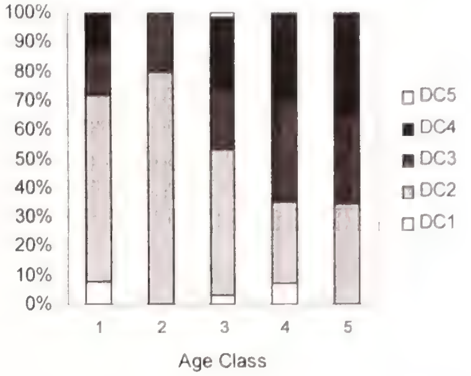

Fig. 1: Correlation between dorsal colouration (DC class 1-5) and associated ventral colourations (VC 1-4) in *Anomalurops beecrofti.*

Colouration and sex

A subsample of 70 males (45%) and 85 females (55%) was available. No significant correlation between dorsal colouration (χ^2 7.585, d.f. 3, P = n.s.) or ventral colouration (χ^2 0.342, d.f. 3, P = n.s.) and sex could be found.

Colouration and age

A total of 160 skins were grouped into age class 1 (16%, n=25), 2 (6%, n=10), 3 (39%, n=62), 4 (25%, n=40), and 5 (14%, n=23). The most reliable results for this relationship were obtained by omitting specimens with dorsal colouration 5 and age class 2. Then the percentage of CEF<5 was 25% and the MEF 1.08. Still the relationship between dorsal colouration and age was not significant (n=149, χ^2 14.226, d.f. 9, P = n.s.).

For the analysis of ventral colouration, the age classes were combined as in the analysis for dorsal colouration. No relationship between ventral colouration and age was found at a percentage of CEF<5 of 38% and a MEF of 2.48.

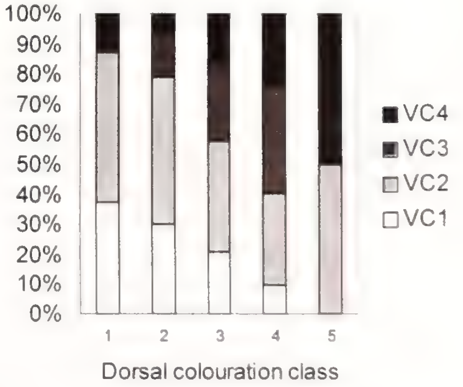

Fig. 2: Correlation between age class and dorsal colouration in *Anomalurops beecrofti.*

However, although no significant relationship for the detailed data set could be found, the dorsal colouration still shows a tendency towards more golden brown with increasing age (Fig. 2). The percentage of the two more silvery colour classes (DC 1, 2) decreases from 72% and 73% in the young individuals, over 54% in the medium, to 37% and 36% in the older specimens. Thus combined, the correlation is also statistically significant (n=159, χ^2 11.380, d.f. 3, $P < 0.05$). For the ventral colouration no tendencies could be observed.

Colouration and collection month

For this analysis two months each were combined (January and February, March and April, etc.) in order to increase the number of specimens per cell. Still 29% of the cells had an expected frequency of less than five and the MEF was 0.72. However, the data did not show a relationship between dorsal colouration and month of collection (χ^2 10.593, d.f. 15, P = n.s.). The same result (χ^2 19.885, d.f. 15, P = n.s.) was obtained for ventral colouration with 54% of the cells having an expected frequency of less than five and a MEF of 1.92.

Colouration and collection area

Localities of collection and summarising diagrams of colouration class frequencies in respective areas are shown in Figure 3 (border lines between these areas are shown in Fig. 6). Uniformly silvery-grey (DC 1) individuals were only found west of the Congo River, from Sierra Leone to Congo Brazzaville. A single specimen (AMNH 86845) labelled as from the Democratic Republic of Congo was caught very close to the Congo River and may as well have been collected on the western bank. The silvery-grey colouration with a narrow golden brown stripe (DC 2) is shown by 43% of the specimens and thus the most frequent. This colouration is distributed across the whole range of the species. The second most frequent colouration (DC 3, silvery grey with a broad golden brown stripe) is found in 28% of the specimens. This colouration is only missing in Angola and adjacent Democratic Republic of Congo. The distribution of the uniformly golden brown individuals (DC 4), which comprise 23% of the investigated specimens, is completely different. They are not found in West Africa but occur frequently in Cameroon, on Bioko, mainland Equatorial Guinea, and Gabon. Further east, isolated records are from Angola and the Democratic Republic of Congo, particularly from the Kivu area. Specimens from Ukaika and Moera in the Kivu region, shown in Plate I (Fig. j), demonstrate the colour variation in one place, ranging from a narrow golden stripe to completely golden brown (DC 2-4). The least frequent colouration (DC 5, uniformly reddish orange) is limited to Equatorial Guinea and the coastal plains of NW Gabon.

The geographic pattern of the ventral colouration differs from that of the dorsal colouration, although a strong correlation between both exists (Fig. 1). Specimens with light underparts lacking orange (VC 1) are found west of the Dahomey Gap and southeast of the Congo and Ubangi rivers but not in between, with the exception of one specimen from Nigeria. In West Africa and south of the Congo River this is the most frequent colouration. Specimens of VC 2 (light underparts with a little orange) occur mainly east of the Dahomey Gap to the Congo River, and replace the lighter specimens of VC 1 in this area. In West Africa and south of the Congo River only a few scattered specimens of VC 2 can be found but more between the Congo and Ubangi rivers. The distribution of individuals of VC 3 (darker ventral colouration) resembles that of VC 2 with slight differences. It is found in Liberia in the West, and then frequently from Cameroon to River Congo and Bioko. South of the Congo River there is a single locality where colourations 1, 2 and 3 are found together. Between the Congo and Ubangi rivers, the relative frequency of VC 3 increases in a NW/SE transect, while that of VC 2 decreases in the same direction. The majority of individuals of VC 4 (uniformly orange underparts) are found from SE-Nigeria to Gabon, and a few between the Congo and Ubangi rivers. Single specimens of this colouration are also found at the periphery of the range, e.g. in Senegal, Togo, and SE-Democratic Republic of Congo.

Statistically significant differences in the frequencies of the respective colourations were found in several neighbouring populations. In West Africa there are three clear-cut barriers where significant differences are found in the DC and VC frequencies. The westernmost border runs along the Volta Rivers in Ghana and separates specimens from Senegal to W-Ghana from those found in E-Ghana and Togo. The second barrier is represented by the Dahomey Gap separating Togo and Nigeria. A third corresponds to the Nigeria-Cameroon border, with the Cross Rivers or the Cameroon mountains being possible geographical barriers. In Central Africa borders are less clear-cut. Along the Sanaga River only the dorsal colouration frequencies show significant differences. The lower Congo and Ubangi rivers separate different frequencies in the ventral colouration, but only the Ubangi is significant for the dorsal colouration frequencies. For specimens from the area between the Congo and Uëlle rivers, a highly significant border in dorsal colouration frequencies exists along the Aruwimi and Ituri Rivers, but this is not true for the ventral colouration. Individuals from the Kivu area are also significantly different in dorsal and ventral colouration frequencies from those found south of the Congo River. No differences in the dorsal colouration were found between specimens from the northwestern parts of this area and individuals from south of the Congo River, and only slight differences (depending on the data combinations) in the ventral colouration. Finally, a significant borderline in dorsal

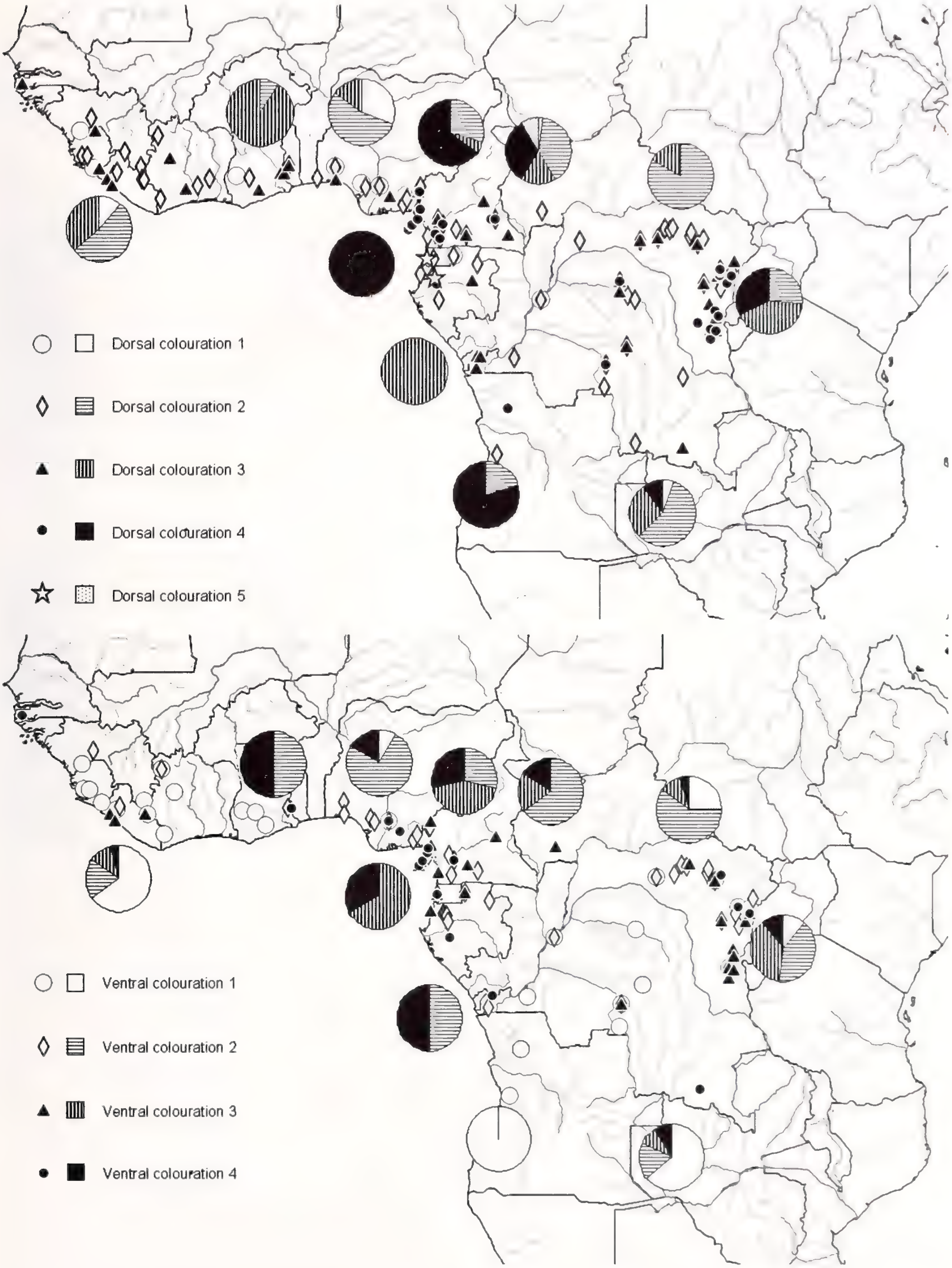
○ ☐ Dorsal colouration 1
◊ ▤ Dorsal colouration 2
▲ ▥ Dorsal colouration 3
● ■ Dorsal colouration 4
☆ ▦ Dorsal colouration 5
○ ☐ Ventral colouration 1
◊ ▤ Ventral colouration 2
▲ ▥ Ventral colouration 3
● ■ Ventral colouration 4

Fig. 3: Geographical distribution of coat colouration in *Anomalurops beecrofti* (see Fig. 6 for border lines).

colouration exists between S-Democratic Republic of Congo and E-Angola. As there is only one ventral colouration type (VC 1) in Angola, no statistical calculation for ventral colour frequencies was possible (the same technical problem applies to the dorsal colouration frequencies on Bioko and in a small area north of the Congo River; see Fig. 3).

3.2. *Anomalurus derbianus*

This species shows the highest variability in colouration (Plate II), ranging from more or less uniformly brownish individuals to specimens with a reddish back, dark grey patagia, black ears and a silvery stripe on the nose. The ventral colouration is much less variable.

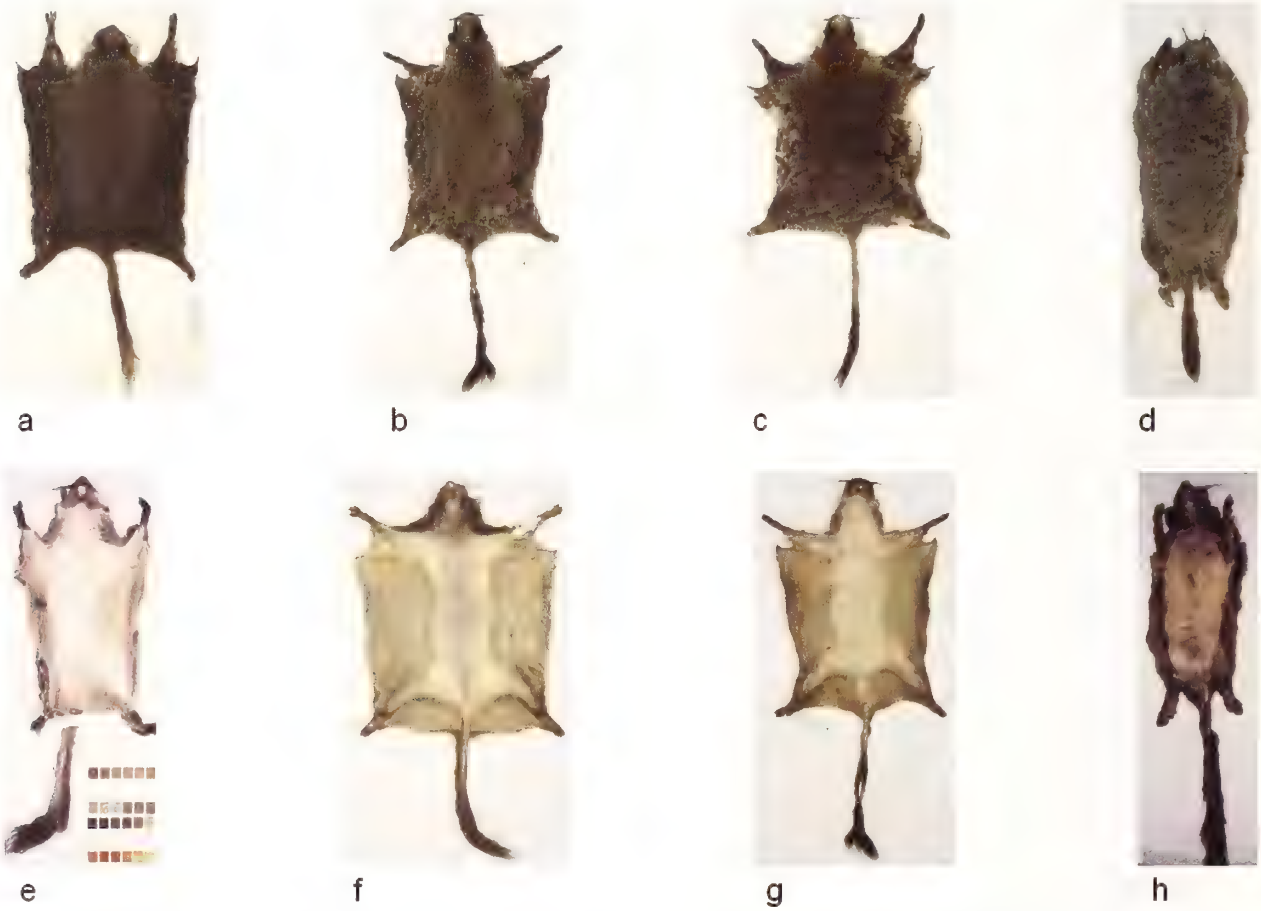

Plate II: Typical representatives of the dorsal and ventral colouration classes in *Anomalurus derbianus* (see text for details). a: dorsal colouration DC 1 (ZFMK 64.491), b: DC 2 (ZFMK 69.148), c: DC 3 (ZFMK 73.363), d: DC 4 (ZFMK 64.817), e: ventral colouration VC 1 (FMNH 88207), f: VC 2 (ZFMK 64.493), g: VC 3 (ZFMK 69.148), h: VC 4 (BMNH 90.6.8.18).

Colouration codes and frequencies

Dorsal colouration (DC):

1. more or less uniformly brown (70%, n=329).
2. back more reddish brown than the rather greyish patagia, no sharp border (19%, n=90).
3. back reddish and patagia dark grey, with sharp border (10%, n=45).
4. silvery grey (1%, n=5).

Ears (E):

1. considerably darker than rest of the head (66%, n=295).
2. more or less the same colouration as the rest of the head (34%, n=154).

Shoulders (S):

1. considerably lighter than neck (42%, n=192).
2. more or less the same colouration as the neck (48%, n=267).

Throat (T):

1. dark ring around neck, mainly closed ventrally (63%, n=85).
2. throat partially light, dark ring ventrally open (37%, n=50).

Ventral colouration (VC):

1. whitish (52%, n=71).
2. greyish without yellow (31%, n=42).
3. yellowish mixed with grey (11%, n=15).
4. light yellow (7%, n=9).

Dorsal and ear colouration

Dorsal and ear colouration show a highly significant correlation. When all character states are used in the analysis, 25% of the cells have an expected frequency of less than five and the MEF is 1.71 (n = 449, χ^2 86.637, d.f. 3, $P < 0.001$). After omitting DC 4, all cells have an expected frequency of more than five and the MEF is 15.20 (n = 444, χ^2 82.553, d.f. 2, $P < 0.001$). The correlation depends on the dorsal colouration class. About half (53%) of the more or less uniformly brown specimens (DC 1) have ears considerably darker than the rest of the head, the others (47%) have ears of the same colour as the head. Individuals with a back slightly (DC 2) or clearly more reddish than the patagia (DC 3) have almost exclusively dark ears (97% and 100% respectively), while most silvery (DC 4) specimens have ears of the same colouration as the head.

Dorsal and shoulder colouration

The correlation for dorsal and shoulder colouration shows results equal to those for dorsal and ear colouration. When all character states are used in the analysis, 25% of the cells have an expected frequency of less than five and the MEF is 2.09 (n = 459, χ^2 194.976, d.f. 3, $P < 0.001$). After omitting DC 4, all cells have an expected frequency of more than five and the MEF is 15.20 (n = 454, χ^2 190.767, d.f. 2, $P < 0.001$). The correlation of dorsal and shoulder colouration also depends on the colouration class. Only 22% of the uniformly brown individuals (DC 1) have light shoulders, but 88% of the specimens with a slightly reddish back (DC 2), and 100% of those with a strongly reddish back (DC 3). None of the silvery individuals (DC 4) have light shoulders.

Ear and shoulder colouration

Ear and shoulder colouration are also significantly correlated (n = 444, χ^2 68.593, d.f. 1, $P < 0.001$). Some 88% of the specimens with light shoulders have dark ears. In the specimens with shoulders of the same colouration as the neck, both types of ear colouration occur equally.

Dorsal and ventral colouration

Correlation between dorsal and ventral colouration appears to be weak. When all four character states for both are used in the analysis, the result is not significant (n = 136, χ^2 14.845, d.f. 9, P = n.s.), but 56% of the cells have an expected frequency less than five and the MEF is 0.13. When DC 4 is omitted from the analysis, 42% of the cells have an expected frequency less than five, the MEF is 0.74 and the result shows a slightly significant correlation between dorsal and ventral colouration (n = 134, χ^2 14.286, d.f. 6, $P < 0.05$). The most reliable results were obtained after ventral colouration 4 was omitted as well. Then the percentage of CEF<5 is 33%, the MEF is 1.20 and the result is significant (n = 125, χ 14.367, d.f. 4, $P < 0.01$). Whitish (VC 1) or greyish without yellow (VC 2) underparts are considerably more frequent than the yellowish colouration (VC 3, 4). Ventral parts yellowish mixed with grey (VC 3) are restricted to uniformly brown specimens (DC 1) and to specimens with slightly reddish backs (DC 2). In individuals with strongly reddish backs (DC 3) the greyish ventral parts without yellow (VC 2) prevail with 73%. The sample of silvery-grey specimens is too small (n=2) for any conclusion.

Ventral and throat colouration

Colouration of ventral surface and throat is significantly correlated (n = 133, χ^2 15.352, d.f. 3, $P < 0.005$). Correlation between general ventral colour and throat colour falls in two groups. Ventral whitish and greyish mixed with yellow specimens have about equally open or closed dark rings around the throat, while more than 80% of ventral greyish without yellow and yellowish without grey specimens have a closed dark ring around the throat.

Colouration and sex

A subsample of 177 males (52%) and 165 females (48%) was studied. No correlation between dorsal or ventral colouration and sex could be shown. When all character states for dorsal colouration are used, the percentage of CEF<5 is 25% (n = 342, χ^2 1.704, d.f. 3, P = n.s.), after omitting DC 4 the CEF<5 is 0% (n = 339, χ^2 1.293, d.f. 2, P = n.s.). The same results are obtained for the ventral colouration; with all character states included the percentage of CEF<5 is also 25% (n = 110, χ^2 0.139, d.f. 3, P = n.s.), and without character state 4, the percentage of CEF<5 is 0% (n = 104, χ^2 0.137, d.f. 2, P = n.s.).

Colouration and age

A total of 365 animals were grouped into age classes 1 (12%, n=42), 2 (21%, n=77), 3 (34%, n=125), 4 (27%, n=99), and 5 (6%, n=22). The correlation between dorsal colouration and age gave best results after colouration 4 was omitted from the analysis. This decreased the percentage of CEF<5 to 20% and increased the MEF to 1.80 with no significant correlation (n = 361, χ^2 12.147, d.f. 8, P = n.s.). Due to the much smaller number of recorded ventral colourations, it was difficult to obtain reliable results. Even when colouration 4 and age 1 were omitted from the analysis, the percentage of

CEF<5 was still 41.7% although the MEF increased to 1.48 (n = 104, χ^2 8.771, d.f. 6, *P* = n.s.). However, the results were not significant in any step of the analysis.

Colouration and collection month

Dorsal colouration and the month of collection showed a significant correlation when two months were combined (January and February, March and April, etc.), and DC 4 was omitted from the analysis (n = 354, χ^2 23.134, d.f. 10, $P < 0.05$). The calculation of an association between ventral colouration and collection month is difficult because of the small number of data for ventral colouration. Most reliable results were obtained by combining three months and by omitting VC 4, thus decreasing the percentage of CEF<5 to 42% and increasing the MEF to 1.90. In this calculation a significant correlation was shown (n = 104, χ^2 14.073, d.f. 6, $P < 0.05$), although not in all steps of the calculation. This somewhat strange result can be explained by the fact that there also is a highly significant correlation between the collection month and the collection area (n = 359, χ^2 100.606, d.f. 20, $P < 0.001$), with a CEF<5 of 13% after combining two months and omitting specimens from Nigeria, the Cameroon mountains, Bioko and the Democratic Republic of Congo south of the Congo River as well as in all previous steps of the analysis.

Colouration and collection area

Localities and summarising diagrams of colouration class frequencies in the respective areas are shown in Figure 4, border lines between the areas in Figure 6. The uniformly brown dorsal colouration is most frequent and occurs across the entire range of *A. derbianus*. From S-Cameroon to the lower Congo and Ubangi rivers, just a few scattered specimens of this colouration are found, while colouration classes 2 and 3 (more or less pronounced reddish back) are well represented. Class 2 (slightly reddish back) is also rare west of the Dahomey Gap but common in the Mamfe area, Cameroon, and on Bioko, where it occurs together with uniformly brown individuals. Specimens with a bright reddish back strongly contrasting with the greyish patagia are restricted to an area from S-Cameroon to the lower Congo and Ubangi rivers. The very rare uniformly silvery colouration is only found in a few localities close to the borders between Democratic Republic of Congo and Zambia, and between Tanzania and Moçambique.

Borders between morphotypes of ear colouration are not clear-cut, but differences in relative frequencies are found. Individuals with dark ears occur frequently from Cameroon to the Democratic Republic of Congo, except for the very south. High numbers of specimens with ears of the same colouration as the head are found in Angola, Zambia, S-Democratic Republic of Congo and Tanzania. This type is rare in Cameroon and Bioko and absent towards the Congo River and in the western half of the Democratic Republic of Congo. Both colouration forms occur together in West Africa from Liberia to Nigeria, in northeastern Democratic Republic of Congo, and in Uganda.

Individuals with light shoulders occur frequently from Liberia to the rivers Congo and Ubangi, and a few are from Bioko, Democratic Republic of Congo and Uganda. Southeast of the rivers Congo and Ubangi, almost exclusively individuals without light epaulettes were collected, but such individuals also occur in a restricted area from S-Nigeria to SW-Cameroon, and on Bioko. There appears to be a cline from light shoulders in West Africa to dark shoulders in the southern and eastern parts of the range.

Distribution of ventral colouration is less clearly related to locality. Specimens with whitish or greyish ventral parts without yellow are found in the whole area inhabited by *A. derbianus*, with higher numbers of whitish individuals west of the Dahomey Gap and from Congo Brazzaville eastward, and more greyish ones from Nigeria to Gabon and on Bioko. Yellowish specimens are much rarer but widespread. Individuals with a ventral colouration mixture of yellow and grey are found in the Ivory Coast, Cameroon, south of the Congo River, and in Tanzania. A few specimens with yellowish underparts without grey were found in Ghana, Cameroon, on Bioko, and in Tanzania. Both yellowish colouration classes are lacking northeast of the Congo River.

Both open and closed dark rings around the throat are distributed over the whole area, with closed markings being more frequent west of the Dahomey Gap, in Bioko, Angola and northeastern Tanzania, and open markings predominating in Zambia and southern Tanzania. From Cameroon to the Democratic Republic of Congo, open and closed dark rings occur in more or less equal numbers. In the area between the Congo and Ubangi rivers, closed dark rings are more frequent in the east and open markings in the southwest.

Clear-cut borderlines between neighbouring populations exist also in *A. derbianus*. Dorsal and ear colouration frequencies in specimens from West Africa do not differ from frequencies in individuals from Nigeria, but both populations differ significantly in shoulder colouration. Specimens from Nigeria and W-Cameroon are significantly different in dorsal colouration frequency but not in shoulder colouration frequency (ear colouration not calculated). Specimens from Bioko are not different from those from Nigeria, but are significantly different from those from W-Cameroon in dorsal and shoulder colouration. W-Cameroon individuals differ significantly from those from S-Cameroon to Congo and Ubangi rivers in dorsal and shoulder colouration. These rivers form a border for dorsal and shoulder but not for ear colouration.

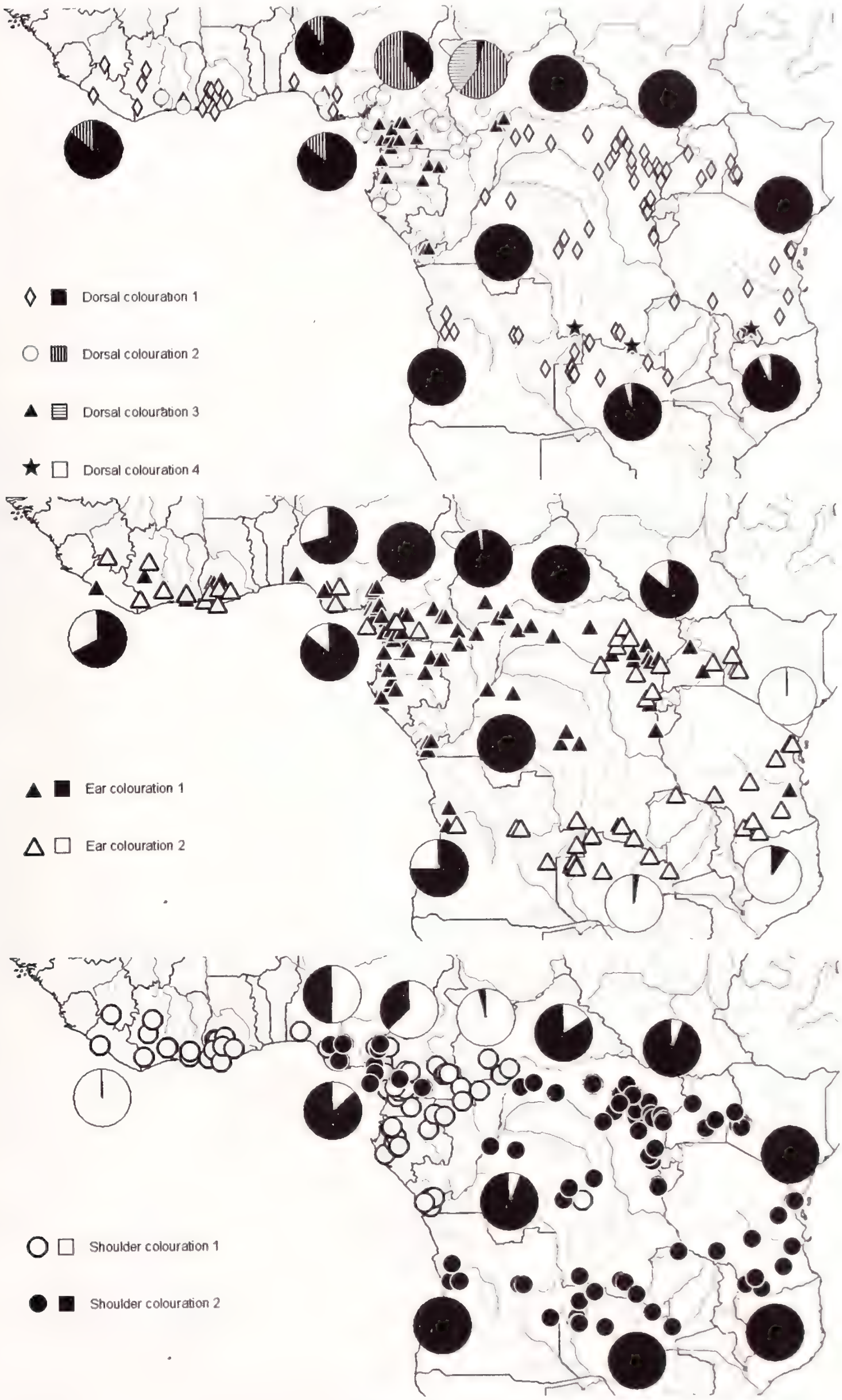
◊ ■ Dorsal colouration 1
○ ▥ Dorsal colouration 2
▲ ▤ Dorsal colouration 3
★ □ Dorsal colouration 4
▲ ■ Ear colouration 1
△ □ Ear colouration 2
○ □ Shoulder colouration 1
● ■ Shoulder colouration 2

Fig. 4: Geographical distribution of coat colouration in *Anomalurus derbianus* (see Fig. 6 for border lines).

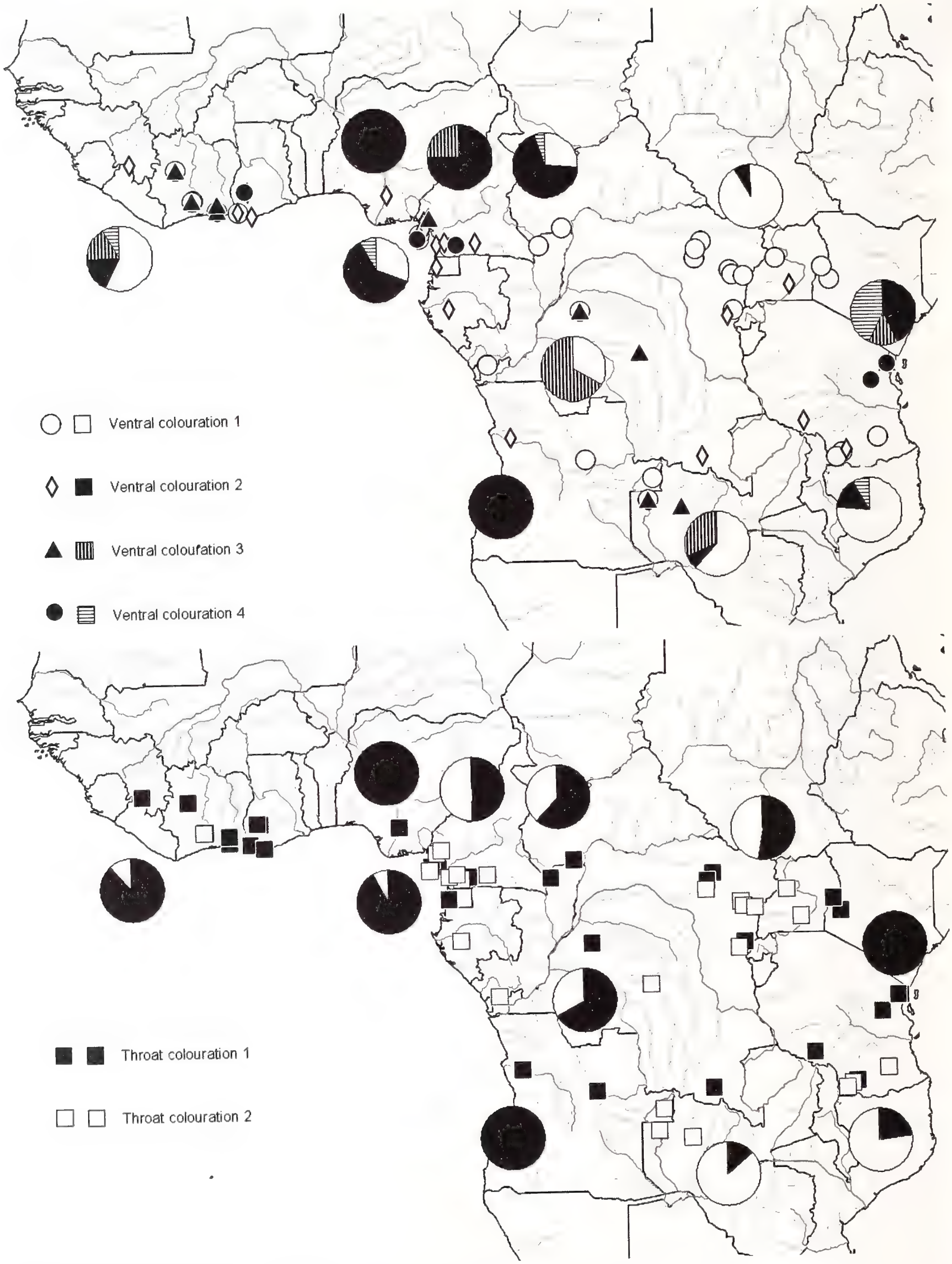
○ □ Ventral colouration 1
◊ ■ Ventral colouration 2
▲ ▥ Ventral coloufation 3
● ▤ Ventral colouration 4
■ ■ Throat colouration 1
□ □ Throat colouration 2

Fig. 4 (continued): Geographical distribution of coat colouration in *Anomalurus derbianus* (see Fig. 6 for border lines).

In N- and C-Democratic Republic of Congo, W-Angola, Uganda and Kenya specimens of *A. derbianus* are remarkably uniform except for a tendency towards ears of the same colour as the rest of the head from NE-Democratic Republic of Congo to Kenya. Finally, one borderline separates specimens from E-Angola, S-Democratic Republic of Congo, Zambia, and Tanzania from the rest of the distribution area. This is best shown by the frequencies of the ear colouration, but it is also parallelled by the occurrence of silvery specimens which are restricted to this southern area.

Differences are less pronounced for the ventral and throat colouration, which is partly due to the smaller data set. This caused problems for a reliable calculation of statistically significant differences. However, in Tanzania specimens from the Usambara Mountains show mainly yellow and yellow mixed with grey underparts, while those from further south are whitish or greyish without yellow.

3.3. *Anomalurus pelii*

This species is generally black with white margins of the patagia, a white tail and a ventral colouration ranging from white to blackish grey. White markings can also be completely absent. The variation in *A. pelii* is mainly defined by the relative portions of black and white (Plate III).

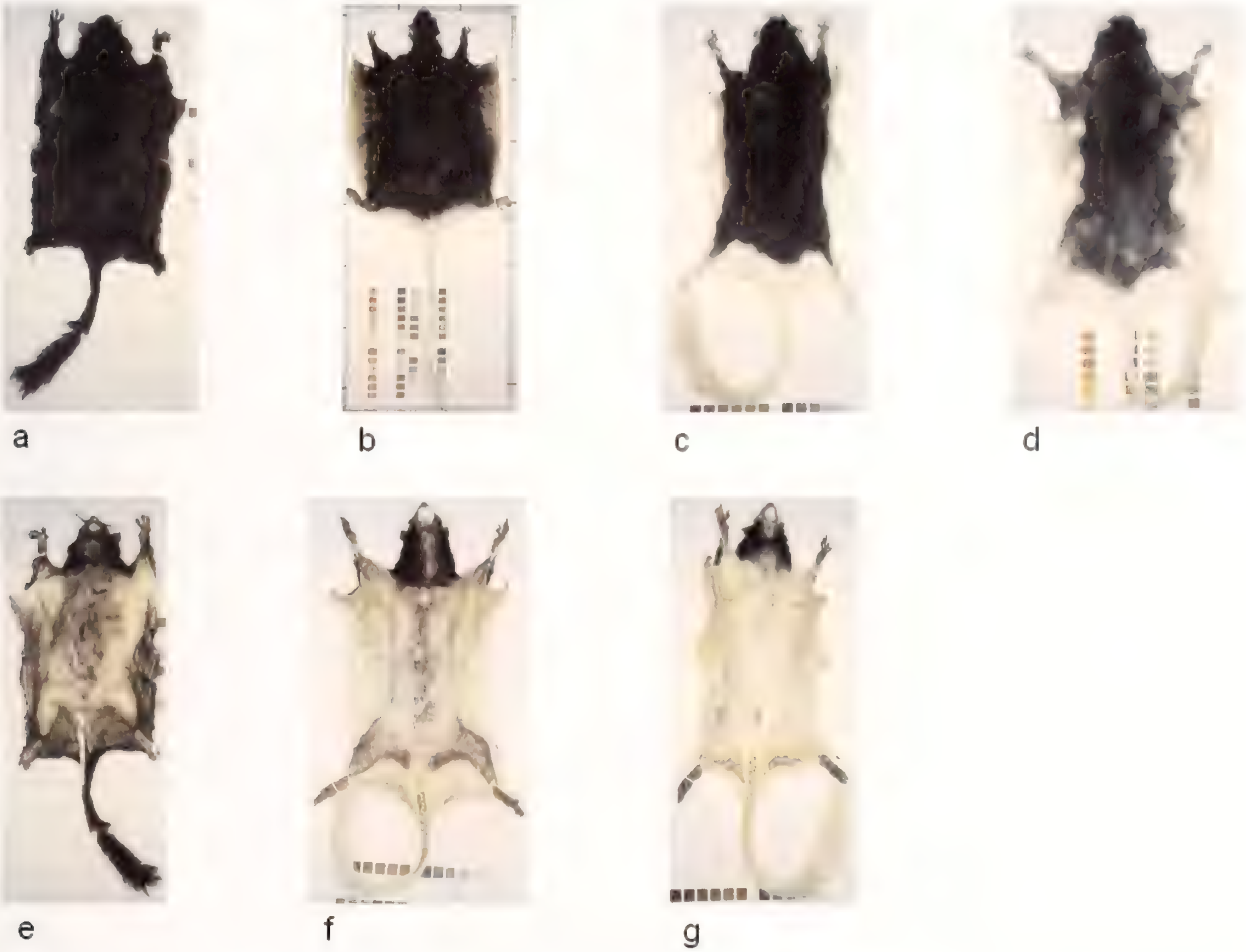

Plate III: Typical representatives of the dorsal and ventral colouration classes in *Anomalurus pelii* (see text for details). a: dorsal colouration DC 1 (ZMA 21.400), b: DC 2 (ZMA 21.262), c: DC 3 (ZMA 21.277), d: DC 4 (ZMA 21.282), e: ventral colouration VC 1 (ZMA 21.400), f: VC 2 (ZMA 21.266), g: VC 3 (ZMA 21.277).

Colouration codes and frequencies

Dorsal colouration (DC):

1. completely black (7%, n=9).
2. white margins less than one-third of pleuropatagia and separated from uropatagia margins (40%, n=55).
3. white margins less than one-half of pleuropatagia, connected with uropatagia margins (23%, n=31).
4. white margins more than one-half of pleuropatagia, shoulder frequently also white (31%, n=43).

Ventral colouration (VC):

1. greyish with blackish central stripe (45%, n=26).
2. white with blackish central stripe (45%, n=26).
3. completely white (10%, n=6).

Dorsal and ventral colouration

A highly significant correlation between dorsal and ventral colouration in *A. pelii* was shown after omitting DC 1 and VC 1 (n = 49, χ^2 13.177, d.f. 2, $P < 0.001$) as well as in all previous steps of the analysis.

In *A. pelii* a correlation between dorsal and ventral colouration is evident, as individuals with a dark dorsal surface tend to be dark on the ventral side, too. The two darker dorsal colouration classes are linked to the darkest ventral colouration in 90% of all specimens, while the relatively rare completely white ventral colouration is restricted to the two dorsal colouration classes with extensive white markings. However, the latter can be combined with every possible ventral colouration, although the darkest colouration is found in less than 12% of the specimens only.

Colouration and sex

A total of 35 males (56%) and 27 females (44%) were available. The data showed no significant correlation between dorsal or ventral colouration and sex.

Colouration and age

Some 117 animals were grouped into age class 1 (5%, n=6), 2 (19%, n=22), 3 (41%, n=48), and 4 (35%, n=41). The data showed no significant association between colouration and age.

Colouration and collection area

Localities and diagrams of colouration class frequencies in the respective areas are shown in Figure 5, border lines between the areas in Figure 6. In spite of the extremely small area inhabited by *A. pelii*, a strong geographic variation exists in the extension of the white markings. West of the Sassandra River only entirely black individuals are found. Specimens with large white markings of the colour classes 3 and 4 are mainly restricted to a relatively small area between the Sassandra and Bandama rivers. In the triangle between the Bandama and Nzi rivers three specimens of the colour classes 2 and 3 were found, thus forming a transition to the area east of the Bandama and Nzi rivers to the Volta River, where exclusively individuals with small white markings of the colour class 2 occur.

3.4. Combined analysis of geographic boundaries

Based on the results shown in Figures 3-5, an attempt was made to identify general borders in the distribution patterns of the characters analysed. Seventeen border lines of different significance for the respective species and colouration characters were recognized (Fig. 6). The Sassandra (Fig. 6, line 1) and Bandama and Nzi (Fig. 6, line 2) rivers obviously are effective barriers for *A. pelii*, but not for *A. beecrofti* and *A. derbianus*. The Volta (Fig. 6, line 3) marks the eastern boundary of the distribution of *A. pelii* and also seems to play a role for *A. beecrofti*. Unfortunately, only very few skins of *A. beecrofti* and none of *A. derbianus* were available from the small area between the Volta and the Dahomey Gap, thus statements concerning this region have to be treated with caution. The Dahomey Gap (Fig. 6, line 4) is a significant barrier for colouration frequencies in *A. beecrofti*, but only the shoulder colouration of *A. derbianus* displays a change there, while dorsal and ear colouration are not affected. An important border line (Fig. 6, line 5) that significantly separates frequencies for almost all investigated characters, except for the shoulder colouration in *A. derbianus*, exists between Nigeria and the highlands of western Cameroon. This highland area differs also from the adjacent plains (Fig. 6, line 6) in the frequencies of dorsal and shoulder colouration of *A. derbianus* and dorsal colouration of *A. beecrofti*. From S-Cameroon to Gabon and SW-Central African Republic, the colouration frequencies are homogenous for *A. derbianus* and quite so for *A. beecrofti*, with the exception of uniformly reddish specimens from a restricted area in the coastal plains of Equatorial Guinea and N-Gabon. Unfortunately very few individuals were collected in Congo Brazzaville, therefore it is not possible to give statements concerning this country. Specimens of *A. derbianus* from the southern tip of South Ogooue (NW of the Congo River, Fig. 6, line 7; see GAUTIER-HION et al., 1999 for definition of the area) show no differences in colouration frequencies to those from S-Cameroon to Gabon. The small sample of *A. beecrofti* from the same area uniformly shows the relatively rare dorsal colouration 3.

Bioko is a special case (Fig. 6, line 8). Specimens of *A. beecrofti* have a uniform dorsal colouration which otherwise is found mainly in W-Cameroon highlands and in Angola. Specimens from Nigeria have completely different colourations. Individuals of *A. derbianus* have identical dorsal colouration frequencies on Bioko and in West Africa (Liberia to Nigeria), but frequencies differ significantly from those of the region between Cameroon and Congo. The frequencies of the ear colouration on Bioko are intermediate to the frequencies in Nigeria and the Cameroon to Congo area. Light shoulders as typical for West Africa occur on Bioko in a frequency intermediate to that of West Africa and Central and East Africa.

The border effect of the lower Congo (Fig. 6, line 9) and Ubangi (Fig. 6, line 10) is also difficult to define. They form clear boundaries for dorsal and shoulder colouration in *A. derbianus*, but not for ear colouration. In

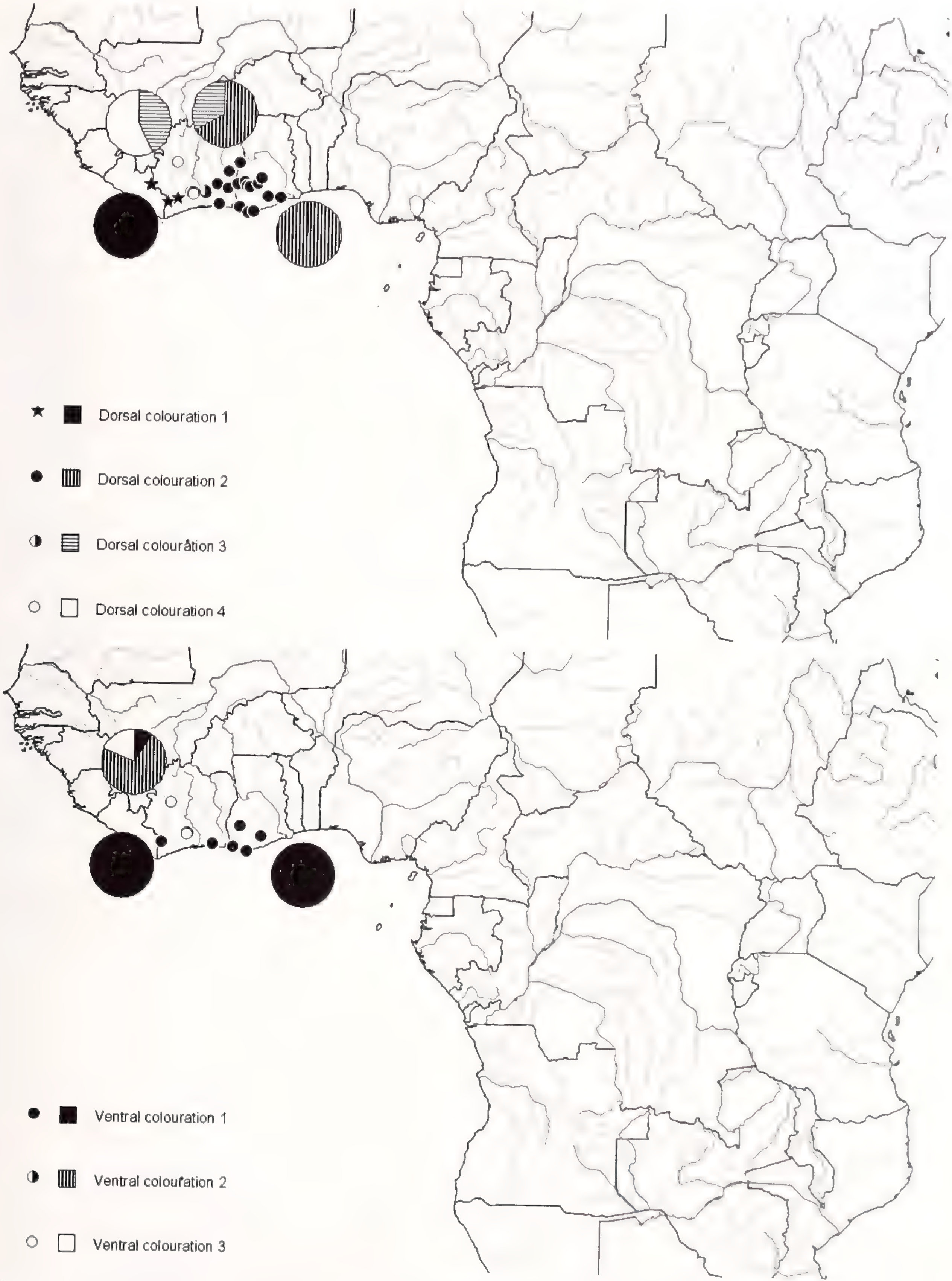
★ ■ Dorsal colouration 1
● ▥ Dorsal colouration 2
◑ ▤ Dorsal colouration 3
○ □ Dorsal colouration 4
● ■ Ventral colouration 1
◑ ▥ Ventral colouration 2
○ □ Ventral colouration 3

Fig. 5: Geographical distribution of coat colouration in *Anomalurus pelii* (see Fig. 6 for border lines).

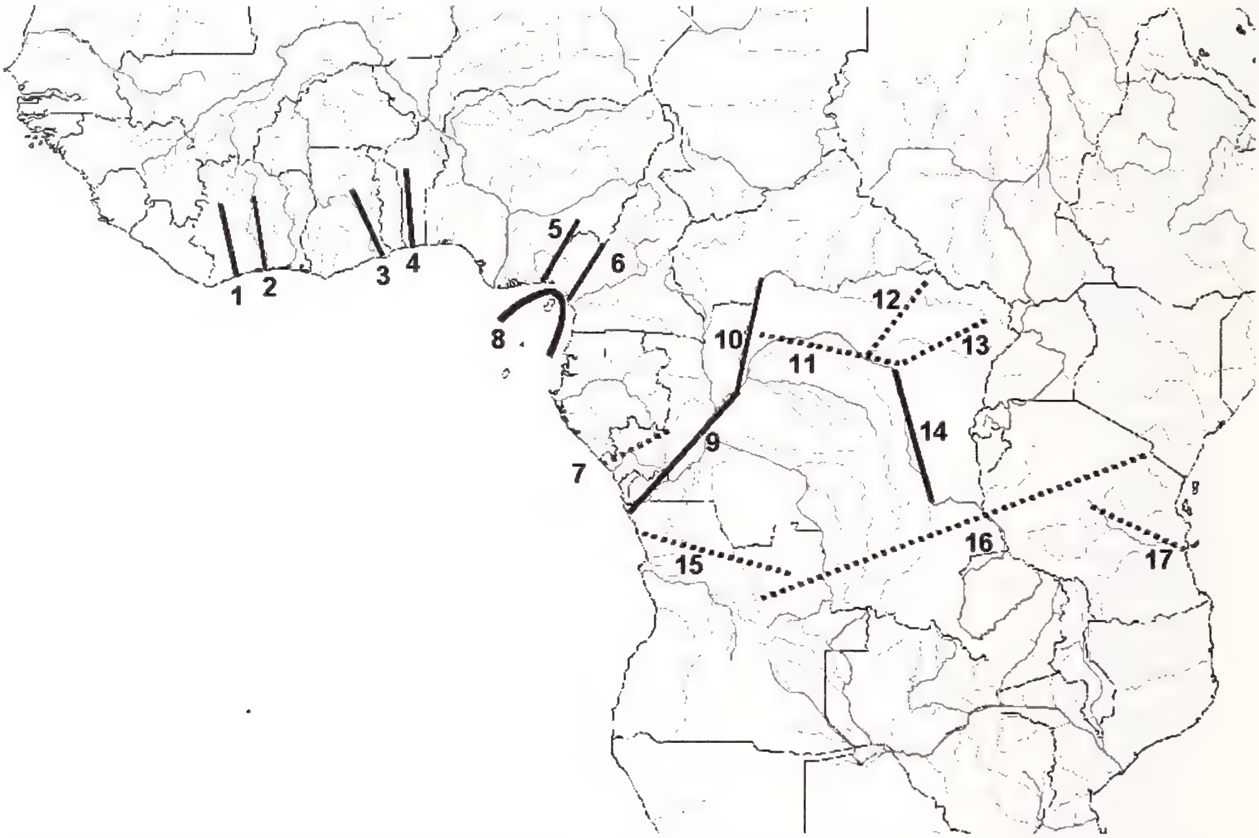

Fig. 6: Border lines of greater (bold) and lesser (dotted) importance for colouration changes in *Anomalurops beecrofti*, *Anomalurus derbianus* and *A. pelii* (see text for details).

A. beecrofti this river system forms a significant barrier for ventral colouration, but only the Ubangi part significantly separates neighbouring populations in dorsal colouration.

Results for the area between the Congo River and the Ubangi, Uëlle, and Kibali river system are also contradictory. For *A. beecrofti*, a significant boundary in dorsal colouration frequencies between the northwestern and southeastern part of the range (Fig. 6, line 13) corresponds to the Aruwimi and Ituri river system, but is not matched by the ventral colouration. Dorsal and shoulder colouration of *A. derbianus* are uniform in this area, but there are differences in ear colouration between specimens from the northwest and souteast (Fig. 6, line 12). However, this boundary lies further west than in *A. beecrofti*. The north bow of the Congo River (Fig. 6, line 11) seems to have no effect on the dorsal, ear and shoulder colouration frequencies in *A. derbianus*. The same applies to the northwestern population of *A. beecrofti*, while southeastern specimens are significantly different from those south of the Congo (Fig. 6, line 14). Specimens of *A. beecrofti* from W-Angola seem to be different from individuals caught in the Congo Basin (Fig. 6, line 15), but the sample size is small. For *A. derbianus* the situation is more complex, because this species occurs also in E-Angola, Zambia, and Tanzania (Fig. 6, line 16). There are only slight differences between specimens from the Congo basin and W-Angola. Light epaulettes are missing in all specimens from Angola, S-Democratic Republic of Congo, Zambia and Tanzania. In the same area (except Angola) the rare uniformly silvery specimens occur, and the highest amount of ears displaying the same colouration as the rest of the head is found here too. In the Usambara Mountains the ventral colouration of *A. derbianus* differs from that of more southern individuals (Fig. 6, line 17).

4. DISCUSSION

Our study has revealed a remarkable mosaic of differences as well as similarities between the respective species. *Anomalurus pusillus*, a species studied but results not shown in detail here, shows a homogeneous brownish colouration throughout its range from Cameroon to E-Democratic Republic of Congo. *Anomalurops beecrofti* varies significantly in the frequencies of the colouration forms but the majority (ca. 70%) of specimens belong to only one of the two colouration forms that occur throughout the distribution area of the species. In *Anomalurus derbianus* the correlation between locality and colouration is more pronounced, although dorsal, ear and shoulder colouration follow slightly different geographic patterns. In *Anomalurus pelii* the dorsal colouration follows clear-cut lines, a pattern not found in any other species.

Despite the particular differences between the species, some general geographic patterns can be extracted. Some boundaries seem to have a major impact on the distribution and frequency of the various colour morphs in the studied species (Fig. 6): The Sassandra, the Bandama-Nzi river system, the Volta River and the Dahomey Gap in West Africa, the highlands of W-Cameroon, the lower Congo and Ubangi river system, and a border line running from Katanga to NE-Tanzania, which separates the southwestern parts of the distribution area of *A. derbianus* from the rest. The Congo River seems to have a low impact on the geographic colouration pattern in *A. beecrofti* and *A. derbianus*, especially in its middle part.

Some of these boundaries are found in other mammalian species as well, but others not. Primates are a well-studied group suited for comparison. Subspecific changes occur frequently in the Ivory Coast, often in the vicinity of the Sassandra River (BOOTH 1958; DANDELOT 1965; GRUBB 1990; LERNOULD 1988; OATES 1988). The Bandama River forms a border between subspecies of *Procolobus badius* (BOOTH 1958; OATES 1988). However, both rivers do not seem to represent barriers for guenons as clear as for *A. pelii*. The Dahomey Gap is a well known border for primates species (BOOTH 1958; GRUBB 1990; LERNOULD 1988; OATES 1988). The highlands of W-Cameroon are a centre of endemism for mammals, and also a border for some guenon subspecies (LERNOULD 1988). Further south, the Sanaga River forms a barrier for many primates (LERNOULD 1988). A further subdivision of the area between the Sanaga and Congo and Ubangi rivers, as found in mitochondrial haplotypes of gorillas (CLIFFORD et al. 2004), could not be observed in anomalurids. The lower Congo and Ubangi rivers are common barriers for numerous primates (DANDELOT 1965; GAUTIER-HION et al. 1999; GRUBB 1990; LERNOULD 1988). In the area between the Congo and Ubangi rivers, no river forms an obvious barrier. However, hybridisation zones or changes of subspecies of primates are frequently found north of the Congo River between the lower Ubangi in the west and the Ituri River and the Kivu region in the east (COLYN 1987, 1988; COLYN et al. 1991; DANDELOT 1965; GAUTIER-HION et al. 1999). The Uëlle River, which marks the northern border of the distribution area of the anomalurids, has the same significance for some primates but not for others (COLYN 1987; GAUTIER-HION et al. 1999; LERNOULD 1988). The Congo River, which delimits the inner Congo Basin to the north and forms a significant barrier for primates (COLYN 1987, 1988; COLYN & DELEPORTE 2002; DANDELOT 1965; GRUBB 1990; LERNOULD 1988) and other mammals, seems to have little importance for the distribution of colour patterns in *A. beecrofti* and *A. derbianus*. The Rift Valley is also a significant barrier for guenons (LERNOULD 1988), and although it seems to have no influence on *A. derbianus*, it is the western border for three other species of anomalurids (*A. pusillus*, *Idiurus macrotis*, and *I. zenkeri*). *Anomalurus derbianus* apparently has a high potential of dispersal as the species not only crosses the Rift Valley but also extends far south into Zambia and Tanzania.

Generally the distribution of coat colouration patterns in anomalurids is strongly correlated with the occurrence of larger rivers. This seems remarkable for animals with an ability for gliding flight. *Anomalurus pelii* has been observed to glide for 50 m (DEKEYSER 1954). Distances of 15 to 20 m (DELANY 1975) and even up to 100 m (KINGDON 1974) were reported for *A. derbianus*, and flights over a distance of 250 m are assumed as possible (KINGDON 1974; MACKAY & CUNNIGHAM VAN SOMEREN 1980). However, larger rivers seem to form barriers that are not regularly crossed. Unfortunately not much is known about the behaviour of anomalurids, but their common way of locomotion is gliding flight from one tree to another, starting from and landing on trunks or branches, and then climbing up the trunk for the next start (ADAMS 1894; KINGDON 1974; RAHM 1969).

What do the observed patterns tell us about the evolutionary history of these anomalurids? First, the patterns are more complex than expected. *Anomalurus pelii* is confined to a small area in West Africa where it established three distinct populations separated by the Sassandra and Bandama rivers (Fig. 5). Although genetic data are not yet available, we assume that reduced gene flow exists between the three populations (SCHUNKE & HUTTERER in press).

The situation in *A. derbianus* and *Anomalurops beecrofti* is more complex (Figs. 3, 4). Some of the patterns agree with biogeographic units identified by COLYN & DELEPORTE (2002) in their analysis of forest guenons. Particularly the West Central faunal area (NW of Congo River to Cameroon Mts) is reflected by the distribution of the anomalurids. COLYN & DELEPORTE (2002) found several subunits in the area, apparently a result of fluctuating savanna and forest vegetation in this area in the Quaternary. The distribution of the shoulder colouration in *A. derbianus* (Fig. 4, bottom) fits this picture. During deteriorating conditions, animals with dark shoulders may have retreated into the Congo Basin and the Cameroon Mts refuge, and animals with pale shoulders into a West African refuge. In times of ameliorating conditions, the West African population dispersed into the former savanna corridor and filled this gap with pale-shouldered animals.

The true picture was certainly more complex, the details, however, must still be filled in. Cladogenesis and secondary hybridization at contact zones have probably obscured the original patterns. The periodic model of cladogenesis in African mammals (GRUBB 1999) seems to be well-suited to explain the current patterns. Genetic data are needed to know to which extent cladogenesis has occurred, and to solve the phylogeography of the group.

Acknowledgements. This publication benefited from the kind help of curators and staff members of the following institutions: Bob Randall, Pat Brunauer, and Nancy B. Simmons (AMNH), Paula D. Jenkins and Daphne Hills (BMNH), Bruce D. Patterson (FMNH), Clem Fisher (LIVCM), Michel Tranier, Jacques Cuisin and Jean-François Ducroz (MNHN), Wim Van Neer and Wim Wendelen (MRAC, Tervuren), Raffael Winkler and Urs Rahm (NHMB), Friederike Spitzenberger and Barbara Herzig (NMW), Olavi Grönwall (NRM), Chris Smeenk (RMNH), Dieter Kock (SMF), Richard W. Thorington, Jr., Michael D. Carleton, Linda K. Gordon, and Helen L. Kafka (USNM), Miguel Vences and Adrian G. Rol (ZMA), and Manfred Ade, Irene Thomas, and Detlef Willborn (ZMB).We thank Jakob Fahr, Gustav Peters, and Bradley Sinclair for constructive criticism of the manuscript. Financial support was provided by the Deutsche Forschungsgemeinschaft (DFG, HU 430/1-1 and 430/1-2). Visits to BMNH and MNHN were funded by the TMR Programme of the European Commission (Bioresource London and Parsyst Paris).

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Table 1: Characters and respective numbers of specimens analysed in this study. *A. pusillus* was not analysed in detail because no appreciable variation exists

Character/Species	**A. beecrofti**	**A. derbianus**	**A. pelii**	**A. pusillus**
Dorsal colouration	227	469	142	128
Ventral colouration	169	137	58	48
Ear colouration	not used	449	not used	not used
Shoulder colouration	not used	459	not used	not used
Throat colouration	not used	135	not used	not used
Sex	156	342	64	not used
Age class	160	365	117	not used
Month of collection	177	359	109	not used
Locality coordinates	208	421	118	113

Bonner zoologische Beiträge | Band 53 (2004) | Heft 1/2 | Seiten 187–191 | Bonn, Juni 2005

Issues in Delimiting Genera in Invertebrates: an Example from the Lepidoptera (Macariini: Geometridae: Ennominae)[1]

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Abstract. Deciding on how inclusive to make genera in Lepidoptera and other invertebrate taxa is scientifically trivial compared with identifying monophyletic groups and building classifications. But the issue is important when making our classifications usable. In this paper, the results of a recent taxonomic review at the genus level of the Geometridae moth tribe Macariini are discussed to highlight some general issues.

1. INTRODUCTION

Professor Clas NAUMANN was a prominent figure, both as the Director of the Museum Alexander Koenig, and as a lepidopterist. This paper is about the importance of taking a global approach to a taxonomic problem that is widely encountered by taxonomists. It was with Clas NAUMANN's strongly international approach to his work in mind that I elected to discuss this general topic. His special interest in Lepidoptera encouraged me to illustrate the generalities by a group of Geometridae moths.

R. A. CROWSON bemoaned the loss of the broad Linnaean concept of the genus (CROWSON 1970). In characteristically waspish mode, he suggested that had systematists admitted intermediate categories between the genus and species they would have shown "a degree of public responsibility and foresight which experience shows is unrealistic to expect of ordinary human beings". A similar approach has been adopted by other authors, who have tried to be more synthetic in their approach (e.g., DAVIS & HEYWOOD 1963, for angiosperms).

With the massive increase in the discovery of species since the time of LINNAEUS, it was inevitable that species would be grouped into ever more clusters. And it was understandable that these clusters would be given generic names, thus splitting the minimal number of genera accepted by LINNAEUS, his contemporaries and slightly later followers. LINNAEUS and his students described species from many parts of the world, not just their native Scandinavia, with many of the specimens collected at trading posts associated with the old shipping lines or the hinterlands of these ports. Nevertheless, their system was founded largely on species encountered in their European surroundings. Division of the genera occurred rather later: for Lepidoptera the process started notably with HÜBNER (1816-[1825]) (EMMET 1991; SCOBLE 1991; HAUSMANN 2001).

Those species of Lepidoptera described by LINNAEUS were assigned to just three genera, *Papilio*, *Sphinx* and *Phalaena*. With the subdivisions of *Phalaena* included, the total number of divisions (call them 'genera') was nine. Today, these divisions are treated mainly as superfamilies (e.g., *Geometra* – Geometroidea; *Noctua* – Noctuoidea). But as large numbers of new species were discovered from outside Europe, those classifications based significantly on European species became unsatisfactory with the consequence that genera became split. New genera were sometimes described for new species with little reference to taxonomic context, particularly where taxonomists were isolated from major European collections. This problem was encountered in a study of the Macariini (SCOBLE & KRÜGER 2002), a tribe of ennomine Geometridae moths distributed worldwide but described originally from Europe, where differences were emphasized at the expense of similarities.

2. THE PROBLEM

The practical problem, which is faced widely by taxonomists working on species-rich groups, is one of how to apply the rank of genus. It is agreed widely among the taxonomic community that each genus should be monophyletic as far as that can be determined. As a scientific problem, the issue of applying rank to the components of a classification is trivial; the more profound question is one of identifying monophyletic groups. But in practical terms applying the rank of genus is not trivial, because the results of taxonomic revision are used not only by taxonomists specialising in areas close to the target taxon, but also by taxonomists working on less closely related taxa, and by a much wider user community with identification and information needs. Taxonomy should be viewed as an information science (GODFRAY 2002), and providing a usable, as well as a formalised, system is a social responsibility. As MABBERLEY (1997) wrote: "... the *Gestalt* of a fig is

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[1] In commemoration of Clas Michael Naumann zu Königsbrück (26.06.1939 - 15.02.2004)

Table 1: Major genus-group concepts of the Marcariini

Guenée [1858]	**Prout (1915-16) Palaearctic**	**Janse (1932) South Africa**	**Wehrli (1939-54) Palaearctic**	**Forbes (1948) New York & Neighbouring States**	**Holloway [1994] Borneo**	**Scoble & Krüger (2002) Global**
Macaria	*Macaria*	*Semiothisa*	*Semiothisa*	*Eumacaria*	*Lampadopteryx*	*Platypepla*
Halia	*Narraga*	**s.l.**	**s.l.**	*Enconista*	*Iridoplecta*	*Milocera*
	Isturgia	(Synonyms	(Subgenera:	*Itame*	*Hypephyra*	*Plateoplia*
	Bichroma	*Macaria, Go-*	*Semiothisa*	*Semiothisa*	*Oxymacaria*	*Narraga*
	Fidonia	*donela, Teph-*	*Godonela*	*Macaria*	*Macaria*	*Heliomata*
	(sensu	*rina* **(in part)**,	*Thyridesia*	*Isturgia*	*Godonela*	*Isturgia*
	Treitschke)	*Osteodes,*	*Neomacaria*	*Mellilla*		*Itame*
	Itame	*Discalma,*	*Macaria*			*Trigrammia*
	Chiasmia	*Peridela*)	*Ligdiformia*			*Mellilla*
	Diastictis		*Chiasmia*			*Dissomorphia*
	Osteodes	*Plateoplia*	*Diastictis*			*Paramelora*
		Platypepla	*Asmate*)			*Eumacaria*
		Hyostomodes				*Gnopharmia*
		Milocera	*Bichroma*			*Oxymacaria*
			Narraga			*Semiothisa*
			Isturgia			*Macaria*
			Itame			*Boarmioides*
			Tephrina			*Parosteodes*
			Gnopharmia			*Chiasmia*
						Malgassothisa
						Lampadopteryx
						Digrammia
						Hypephyra

usually unmistakable but to split the genus *Ficus* into several on the basis of characters only revealed by lenses seems academic self-indulgence."

The problem has arisen through a combination of two frequently observed characteristics of taxonomy. First, taxonomy is the product of a long history with a scattered literature. Second, because many taxonomists lack access to comparative material (specimens and literature), a lack of context is often apparent. For about 100 years after LINNAEUS (1758) published the tenth edition of *Systema Naturae*, a relatively small number of species were described (Fig. 1) and by few taxonomists. With the explosion of exploration from the mid 19th Century there was a corresponding increase in collection of specimens and in the description of species. The rate of species description fell around the mid 20th Century and taxonomy entered a more synthetic phase where species were synonymised or recombined with new genera. The emphasis on accepting only monophyletic taxa as valid and worthy of naming, gave an apparent intellectual basis for splitting taxa until all recognised groups were monophyletic. Currently there is a welcome emphasis on the value of taxonomy to a wider user community, which should encourage taxonomists to integrate further their efforts and to be prepared to synthesise.

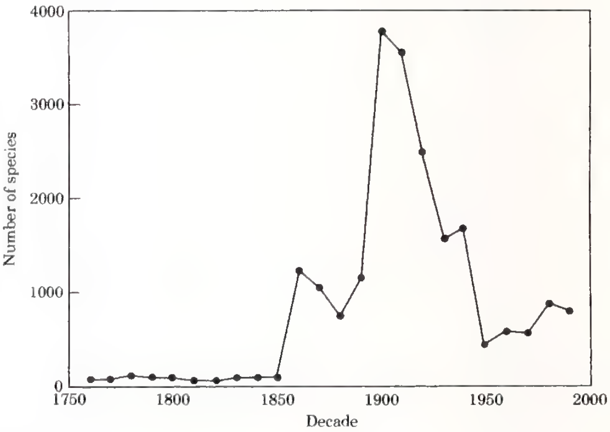

Fig. 1: Graph of number of species of Geometridae described by decade since 1758 (simplified from GASTON et al. 1995).

I use the results of a genus-level study (SCOBLE & KRÜGER 2002) for the geometrid moth tribe Macariini to exemplify some issues faced by taxonomists classify-ing taxa that are widely distributed. From this basis some general messages are presented.

3. THE TRIBE MACARIINI

There are about 700 species of Macariini, a tribe belonging to the subfamily Ennominae of the Geometridae. The group includes medium-sized geometrid moths and is represented in all biogeographical regions. The larval foodplants of many species belong to Leguminosae (Fabaceae). The moths are encountered frequently in light traps.

The tribe was described (as 'Macaridae') by GUENÉE [1858] for four genera, two of which are now excluded from the tribe. Six prior regional works had a significant influence on the global generic classification proposed by SCOBLE & KRÜGER (2002), the genera accepted in each publication being listed in Table 1. Neither PROUT (1915-16), JANSE (1932), nor WEHRLI (1939-54) united their genera under a tribal division, but they indicated that the genera were associated. JANSE (on the South African species) included all the large macariine genera under *Semiothisa* (including *Macaria*, which has priority), starting a tradition that has been followed to the present day by many lepidopterists understandably confused by the plethora of names and unclear generic concepts. WEHRLI (Palaearctic fauna) recognised more taxonomic structure than did JANSE, treated JANSE's synonyms as subgenera of *Semiothisa*, and added several other subgenera. FORBES (1948), in the few genera treated in his restricted area of New York and neighbouring States, included all genera with the characteristic uncus 'horns' in *Semiothisa*, noting that the genus was enormous and of world-wide distribution. Unfortunately both Janse and Forbes were unaware that the type species of *Semiothisa* lacks 'horns' and has genitalia that are distinctive, the genus being exclusively neotropical and having 18 other members. Thus *Semiothisa* in their sense is equivalent to *Macaria* plus *Chiasmia* in the sense of SCOBLE & KRÜGER (2002).

The genera accepted by SCOBLE & KRÜGER (2002) are also listed in Table 1. These authors concluded that the Macariini are not certainly defined as a monophyletic group – the boundaries are unclear. There appear to be two large, arguably monophyletic genera (*Macaria* and *Chiasmia*), and one large genus (*Isturgia*) that is less convincingly monophyletic. Within these genera occur several well-defined subgroups. Within the other Macariini there are a number of small and probably monophyletic genera.

4. RESULTS OF THE GLOBAL GENERIC REVIEW

Taxonomic treatments of the genera are found in the review (SCOBLE & KRÜGER 2002), but for the purposes of this account a few key results are highlighted.

Macariini are not defined perfectly as a tribe, but the species can be recognised by their expression of one or more of three characters: a divided valva; stout setae ('horns') on the uncus in the male genitalia; and chaetosemata extended across the head. In many species the eighth abdominal sternum is cleft, excavated or emarginated. A further possible character is the presence of a fovea, a raised cuticular patch at the base of the forewing in males largely denuded of scales, but the taxonomic value of this structure is not established. The core genera of the Macariini are properly associated, but the association of certain genera within the Tribe remains questionable.

We treated many generic names as synonyms. Of the three largest genera *Chiasmia* has 12 synomyms, *Macaria* 16 and *Isturgia* three. These were among the earliest to be described for the tribe, and were erected for European species. Discoveries of material from other continents led to the description of new genera without detailed comparisons being made with type species of the European genera.

There are, among Macariini, species with similar wing pattern and colour that fall into quite different genera when genital morphology is compared. This is unsurprising given that the early genera were described on 'facies' alone. Consequently, macariine taxonomy suffered both from a multiplicity of inadequately defined genera and from the erroneous generic assignment of many of the species. As a result of the confusion, many lepidopterists simply, and understandably, used one genus, *Macaria* (or, incorrectly, *Semiothisa*), in which to place most macariine species.

The revised classification proposed was intended to reflect best the considerable amount of taxonomic structure apparent within the Macariini. Most species fall into one of three large genera - *Chiasmia*, *Macaria* or *Isturgia*. Species are included that look quite different in external appearance within the same genus, but morphological similarities suggest their association. Within these genera several species groupings were noted. There are a number of well-defined smaller genera of which the genus *Semiothisa* is one. Thus the revised classification is a compromise between placing most species in a massive single genus '*Semiothisa*' (in the incorrect sense of many authors) and creating numerous genera for small clusters of species or single species. The principle, however, of trying to recognise only monophyletic groups remains.

5. MESSAGES

Taxonomists will be familiar with the issues we encountered in revising the Macariini. The general points that arose are as follows.

1. Much taxonomy is focused on the fauna of a particular region. While it is perfectly reasonable to undertake faunal studies, taxonomists bear a responsibility to execute their work in a broad context. An excellent contemporary example of how a faunal review can be written within a strongly contextual taxonomic framework is the multi-volume treatment of the *Moths of Borneo* by J. D. HOLLOWAY (e.g., HOLLOWAY [1994], which includes Macariini). Holloway treated the Macrolepidoptera moths of the region to the level of species, but made extensive comparative studies across S E Asia and Australasia and, using the rich collections of the Natural History Museum, London, provided a global context.

A practical problem arises in that many taxonomists work remotely from major comparative reference collections and libraries. If those of us based in such collections expect such a comparative approach from others, we shall need to provide better access to the comparative information by creating cross-institutional infrastructures. The Internet will be the medium through which this infrastructure is delivered.

2. It is preferable not to describe new genera for single species or small groups of species unless they fall demonstrably outside the generic system currently in use. Classifications and names do and should change, within reason, when research shows existing systems are not optimal. However, taxonomists should be sensitive to those who use their results. We must be ever more conscious of that wide community that uses our results and ask ourselves: "will the changes we make to classifications help or hinder those who use the classifications?" With careful thought there should be no reason why we should compromise on scholarship.

Where uncertainty exists as to the generic association of a species, placing inverted commas around the genus name adopted can be a helpful convention to indicate that the species should probably be excluded. This protocol avoids the need to create new genera, but indicates that further study is required. For example, "*Semiothisa*" *nigroalbana* Cassino implies that the generic placement of *nigroalbana* is uncertain. This simple modification avoids the complexity of discarding the binomial system as suggested, for example, by MICHENER (1964), yet protects the integrity of monophyletic groups.

Like MICHENER, many taxonomists (myself included) have probably felt at times that we might be better off cutting the requisite nomenclatural link between genus and species. Such a break would enable species to be described without them having to be assigned to a genus when their associations remained unknown. The advantage of the proposal would obviate the need either to associate each species with an existing genus or to describe a new genus for every unassociated species. However, the cost of abandoning the binomial system of nomenclature would be heavy. Loss of a standard that has served taxonomy so well for 250 years is likely to lead to confusion. Moreover, with increasing computerisation of taxonomic information the established link between genus and species is one that is embedded in many databases.

3. Taxonomists frequently encounter the situation where a large genus includes a number of demonstrably monophyletic subgroups and also many single species unassociated with any others. The use of informal species-groups within a genus can be helpful to indicate taxonomic structure within such a genus without the need to describe a new genus for each subgroup or for each unassociated species. In the macariine exemplar, several subgroups, often closely related species from the same area, are evident in the three large genera, *Macaria*, *Chiasmia* and *Isturgia*, alongside numerous unassociated single species.

4. In nearly all higher taxa we find genera for which the monophyly is convincingly well founded and many genera where it is not. An argument for splitting a genus that is not demonstratively monophyletic into better-established monophyletic genera, and as many further genera as there are unassociated species, is that the situation might best reflect the natural pattern. However, taxonomists would do well to follow this course of action only where the original genus is demonstrably not monophyletic.

5. The taxonomic history of a group helps one understand problems of classification. Bacterial (prokaryote) taxonomy was re-based in 1980 (in effect, a new *Systema Naturae* was created for bacteria) because so many type cultures had been lost that few names could be referenced to specimens (SNEATH 1986). But such is not the case for Lepidoptera taxonomy, where types dating from the time of LINNAEUS still exist. Taxon concepts often have a long history, and there seems little to be gained and much to be lost by discarding the insights and information associated with those concepts (e.g., PULLAN et al. 2000; YTOW et al. 2001; BERENDSOHN 2003). Therefore, any review of genera (or any other taxonomic rank) in Lepidoptera (and most other eukaryote organisms) requires that we examine the different systems through time. Proposing new classifications without understanding how previous taxonomists came to their conclusions leads to poor taxonomy.

6. CONCLUSION

The description of all species of organisms is a worthy goal, but an immense undertaking, particularly when microorganisms are brought into consideration. Indeed description is not a single process, but requires both recognition that a putatively new species is actually undescribed and also its assignment to the appropriate genus - the generic name being a part of the name of the species. To say that a species should not be described in a taxonomic vacuum may sound like stating the obvious, yet the number of new species described within an inadequate generic framework is significant. Material advances in our understanding of Lepidoptera biodiversity can be made more rapidly by focusing on generic reviews on a global or large regional basis, as has been done over the last decade on Geometridae (e.g., PITKIN 1996, 2002; SCOBLE 1995) including the work on the Macariini discussed in this paper. An advantage of this approach is that it accelerates coverage of Lepidoptera biodiversity while at the same time improving the quality of the taxonomic framework. Such studies will better equip those taxonomists with access to collections that are regional in scope to undertake work on species within their geographical domain.

A further reason for good quality taxonomy of higher taxa was expressed by WILLIAMS & GASTON (1994) who discussed the use of higher taxa as surrogates for biodiversity assessment (for summary see http://www.nhm.ac.uk/science/projects/worldmap/refs/key.htm#key4). They concluded that "With careful choice of higher-taxon rank, it may be possible to re-deploy effort from taxonomically intensive to taxonomically extensive surveys, in order to estimate the global distribution of a much larger proportion of overall biodiversity at the same cost".

Acknowledgements. I thank Linda Pitkin, Natural History Museum, London, for reading a draft of this manuscript and for her collaboration on Geometridae taxonomy over the years.

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Bonner zoologische Beiträge	Band 53 (2004)	Heft 1/2	Seiten 193–209	Bonn, Juni 2005

Revision of the *Trichoclinocera dasyscutellum* Group from East Asia (Diptera: Empididae: Clinocerinae)[1]

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Abstract. The *Trichoclinocera dasyscutellum* group is revised and includes the following eight species: *T. asiatica* sp. nov., *T. dasyscutellum* (Saigusa), *T. feuerborni* (Engel) comb. nov., *T. fluviatilis* (Brunetti), *T. naumanni* sp. nov., *T. nepalensis* sp. nov., *T. taiwanensis* sp. nov., and *T. yunnana* sp. nov. This group is restricted to East Asia, ranging from Nepal to Japan and as far south as Java. Male genitalia are illustrated and a key to species is provided. *Clinocera velutina* (Engel), originally published together with *T. feuerborni*, is also redescribed. Lectotypes are designated for both species.

Key words: Taxonomy, aquatic, new species, morphology, genitalia

1. INTRODUCTION

The genus *Trichoclinocera* Collin is among the most commonly collected clinocerines in North America and Japan. They are normally encountered on emergent rocks in large streams and rivers, usually where the riparian vegetation is open overhead (SINCLAIR 1994). Adults fly close to the water surface in search of prey and consequently are difficult to collect by sweep net and rarely taken in malaise traps. They are most readily collected by use of an aspirator, sucking up individual specimens that are found sitting on emergent rocks in the stream.

There are currently 24 described species found in the Nearctic, Palearctic and Oriental Regions (SINCLAIR 1994, 1995), plus a recently described species from India (WAGNER et al. 2004). The genus was thoroughly redescribed and divided into six species-groups by SINCLAIR (1994). The *T. dasyscutellum* group, the focus of this paper, is considered the sister clade to the western North American *T. comata* group on the basis of setulae on the scutellum. The recently described species, *T. serrata* Wagner & Leese, 2004 lacks this feature and can not be assigned to the *T. dasyscutellum* group, and is most closely related to *T. cyanescens* Vaillant, 1960.

Numerous congeneric species from East Asia await description and this paper is the first of a series of studies of this genus from this region. This study is dedicated in the memory of our colleague and fellow entomologist, Dr. Clas M. NAUMANN.

2. MATERIALS AND METHODS

This study is based on some 1600 specimens borrowed from or deposited in the following institutions: Biosystematics Laboratory, Kyushu University, Fukuoka, Japan (BLKU); The Natural History Museum, London, England (BMNH); Bernice P. Bishop Museum, Honolulu, USA (BPBM); Canadian National Insect Collection, Ottawa, Canada (CNC); Hungarian Natural History Museum, Budapest (HNHM); Faculty of Agriculture, Hokkaido University, Sapporo, Japan (HUS); Staatliches Museum fur Naturkunde, Stuttgart, Germany (SMNS); Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany (ZFMK); Zoological Survey of India, New Alipore, Calcutta, India (ZSI).

Terms and methods used in specimen preparation follow that of SINCLAIR (1994, 1995). The use of a very mild acid (e.g., lactic acid) for clearing and studying the genitalia of male *Trichoclincera* is very important. Strong acids such as KOH often destroy the delicate membranous tip of the phallus. The following abbreviations are used in the description: acr - acrostichal setulae; dc - dorsocentral bristles; dm - discal medial; npl - notopleural bristles; pal - postalar bristles; ph - posthumeral bristle; pprn - postpronotal bristles; presut spal - presutural supar-alar bristles; psut spal - postsutural supra-alar bristles; R - radial vein; sctl - scutellar bristles; T - tergite. Also the following abbreviations are used for the most frequent collectors' names: J. Emoto - JE; R. Matsumoto - RM; H. Shima - HS; B.J. Sinclair - BJS; T. Saigusa - TS.

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[1] In commemoration of Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004)

3. TAXONOMY

3.1. *Trichoclinocera dasyscutellum* group

This species group is distinguished from other species of *Trichoclinocera* by the following suite of characters: long, slender legs; pronounced rows of stout ventral bristles on the fore femur absent; normally only spine-like preapical bristles present on femora (Figs. 22-27); lacking anterodorsal and posterodorsal leg bristles; scutellum with setulae on disc; face generally flat, with small apical notch (Fig. 19); cell dm produced apically, not truncate; surstylus normally with scolex-like apex; phallus with short, elaborate membranous apical lobes.

3.2. Key to species of the *Trichoclinocera dasyscutellum* group

1 Dorsocentral bristles longer than ocellar bristles or two-thirds length of antennal arista-like style........... 2

– Dorsocentral bristles shorter than ocellar bristles or one-half length of antennal arista-like style.............. 3

2 Hind tibia with posterodorsal spur-like bristle one-third from base; one slender lower notopleural bristle; clasping cercus tapered and narrow apically (Fig. 2) (Japan).......................... *T. dasyscutellum* (Saigusa)

– Hind tibia without spur-like bristle; 2-3 stout lower notopleural bristles; clasping cercus rounded apically (Fig. 1) (South Korea, Russia: Primorsk Territory) .... *T. asiatica* sp. nov.

3 Pleura brown, lacking distinct blue pruinescence....... 4

– Pleura with distinct blue pruinescence...................... 6

4 Radial vein with 3-5 erect bristles proximal to origin of Rs, ca. one-half length of basal costal bristle, in addition to setulae (Java) ...... *T. feuerborni* (Engel) comb. nov.

– Radial vein with setulae only, lacking long erect bristles 5

5 Male fore femur with two black, spur-like anteroventral subapical bristles and posteroventral row of numerous stout bristles, those on basal half nearly subequal to width of femur; clasping cercus strongly hooked and tapered; surstylus with scolex-like apex (Fig. 6); female fore femur with 3-4 distinct spur-like subapical bristles (China).......... *T. naumanni* sp. nov.

– Male fore femur with one black, spur-like anteroventral subapical bristle and a sparse posteroventral row of pale hairs, those on basal half less than width of femur (Fig. 25); clasping cercus finger-like, slightly curved; surstylus with subapical pointed projection and stout apical bristle; female fore femur with one distinct spur-like subapical bristle (Fig. 8) (Nepal, Vietnam).................................. *T. nepalensis* sp. nov.

6 Base of stalk of halter brown, not brightly coloured; anterior apex of phallus with long, slender pointed membranous sac (Fig. 10) (Taiwan) .... *T. taiwanensis* sp. nov.

– Base of stalk of halter bright orange-brown; anterior apex of phallus with short, broad membranous sac (females difficult to distinguish beyond this couplet) 7

7 Clasping cercus straight beyond base, tapered only at extreme apex; length of surstylus less than half length of cercus with narrow angular basal prolongation (Fig. 5) (India, Nepal, China: Yunnan)............... .... *T. fluviatilis* (Brunetti)

– Clasping cercus arched throughout length, apical fourth tapered to slender apex; length of surstylus more than half length of cercus with rounded (Fig. 11) or broad angular basal prolongation (China, Vietnam)..................................... *T. yunnana* sp. nov.

3.3. *Trichoclinocera asiatica* sp. nov. (Figs. 1, 7, 22)

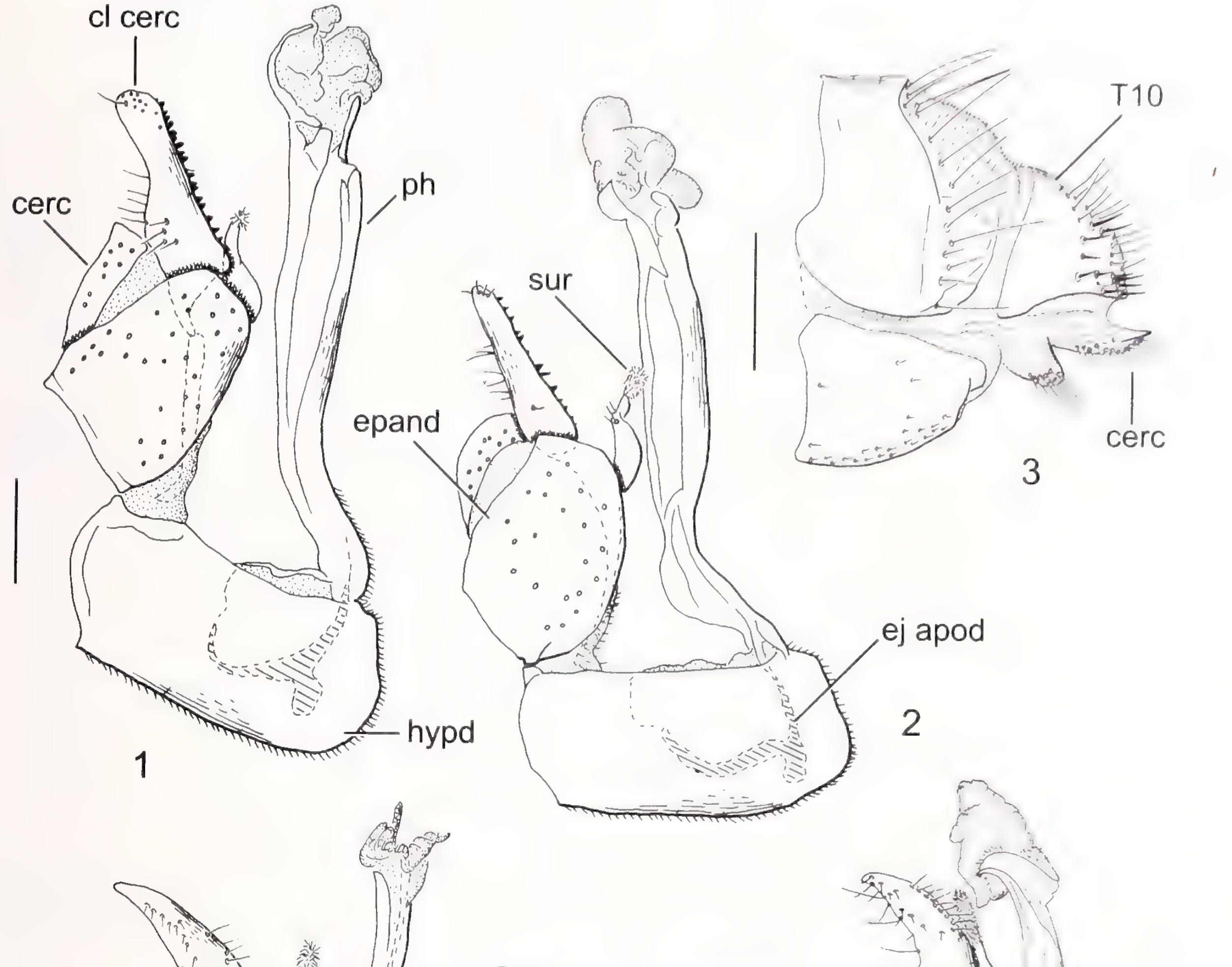
Type Material. Holotype male labelled: "USSR: Primor'ye/ 17km SSW of/ Krounovka, 140m/ 29.vii.1990/ T. Saigusa leg." (BLKU).

Paratypes: RUSSIA: 141 ♂, 299 ♀, 28-29.vii.1991, same data as holotype (BLKU); 23 ♂, 58 ♀, Primorskij Kraj [Primorsk Terr.], SW Krounovka, nr. Mt Medvezh'ja, 8-9.vii.1993, T. Yasunaga (BLKU); 2 ♂, 9 ♀, Primorskij Kraj, SW Krounovka, nr. Mt Medvezh'ja, 4-6.vii.1993, T. Nakamura (BLKU). SOUTH KOREA: 1 ♂, Samjeong, Hwagae-Myeon, 600-800 m, 8.vi.1991, TS (BLKU). Several specimens deposited in ZFMK.

Recognition. This species is distinguished by its yellowish coxae, long dorsocentral bristles and 2-3 stout, lower notopleural bristles.

Description. Wing length 3.6-4.2 mm

Male. Brown in ground colour. Head rounded; compound eye large, rounded. Face narrowest at middle, ca. width of antennal sockets, with bright blue pruinescence, lower margin of face nearly straight (clypeus) lacking pronounced carina or notch; width of gena one-sixth height of eye. Anterior margin of ocellar triangle, lateral postocciput and gena with blue pruinescence; vertex and upper part of postocciput dark when viewed dorsally. Ocellar bristles longest among cranial bristles; occiput with 3 pairs of bristles posterior to ocellar triangle, ca. one-half length of ocellar bristles; postocular with row of short bristles along margin of eye, upper 3-4 bristles darker and more stout than lower bristles. Arista-like stylus short and slender, slightly tapered apically. Palpus slender, length less than one-half height of eye.



Figs. 1-6: Terminalia of *Trichoclinocera dasyscutellum* group. (1) *T. asiatica* sp. nov., male; (2) *T. dasyscutellum* (Saigusa), male; (3) *T. dasyscutellum* (Saigusa), female; (4) *T. feuerborni* (Engel), male; (5) *T. fluviatilis* (Brunetti), male; (6) *T. naumanni* sp. nov., male. Scale bar = 0.1 mm. Abbreviations: cerc - cercus; cl cerc - clasping cercus; ej apod - ejaculatory apodeme; epand - epandrium; hypd - hypandrium; ph - phallus; sur - surstylus; T - tergite.

Pleura and lateral margin of scutum, including postpronotal lobe and notopleuron entirely clothed in blue pruinescence; posterolateral corner of scutum near postalar ridge somewhat paler. Thoracic bristles long, some longer than width of eye; several acr anterior to first dc; 5 pairs dc; 1 pprn; 1 presut spal; 1 upper, 2-3 stout lower npl; 1 psut spal; 1 pal; 2 pairs sctl and numerous pale setulae on disc; several pale bristles on notopleural depression. Laterotergite with patch of pale bristles; prothoracic episternum, katepisternum, and hind margins of metepisternum with long, pale hairs.

Wing narrow, infuscate; narrow, faint, parallel-sided stigma present. One long, basal costal bristle, subequal to length of posterior dc. Row of setulae from base of R to tip of R_1; cell dm strongly produced apically; R_4 and R_5 divergent apically. Halter dark with pale base.

Legs with femora pale brown beneath and basally, becoming darker toward apex. Coxae with long pale, marginal hairs; fore coxa yellowish with blue pruinescence on basal half; mid and hind coxae somewhat pale with blue pruinescence. Fore femur with row of 6-7 slender anterior bristles on apical third (Fig. 22), dorsal to spine-like bristles; antero- and posteroventral row of pale, slender bristles along entire length, posteroventral setae subequal to width of femur, twice length of anteroventral bristles; 3 black, very short, peg-like anteroventral bristles on apical third; anterodorsal region with row of 5-6 stout, black bristles on basal third. Fore tibia with biserial row of short, stout bristles beneath. Mid femur with 3 pairs of black, spine-like antero- and posteroventral preapical bristles, nearly as long as one-half width of femur; anterior margin with long, slender bristles along entire length, longer than width of femur; lacking erect antero- and posterodorsal bristles. Hind femur with 2-3 pairs of antero- and posteroventral preapical bristles, less stout than preapical bristles of mid femur; lacking antero- and posterodorsal bristles. Hind tibia with 3-4 erect, spine-like dorsal and ventral bristles on apical third, longer than width of tibia. Tarsi longer than corresponding tibiae. Empodium pulvilliform, subequal in length to claw, less than one-half length of tarsomere.

Hypandrium (Fig. 1) long and cylindrical, longer than epandrium. Phallus long, distinctly bent sub-basally; apex with slender, curved anterior process and pair of straight, short, rod-like posterior processes; ejaculatory apodeme strongly recurved anteriorly. Surstylus very slender, somewhat twisted and arched medially, with membranous oval scolex-like apex. Clasping cercus slender, finger-like, parallel-sided, with rounded apex; row of stout, peg-like bristles on inner dorsal margin.

Female. Similar to male except as follows: stout anteroventral bristles on apical third of fore femur longer and stouter. Terminalia very similar to *T. dasyscutellum*: sclerites of segment 8 narrowly separated laterally; T8 with posterior row of long and short bristles, length of dorsal bristles subequal to length of sclerite; T10 with stout, curved bristles on posterior half, with 3-4 apical bristles more stout than remaining bristles; anteroventral corner of T10 not narrowed and prolonged.

Geographical Distribution and Seasonal Occurrence. This species occurs in the far east of Asia, specifically the Primorsk Territory of Russia and the Korean Peninsula (Fig. 7).

Remarks. See under *T. dasyscutellum*.

Etymology. The specific name refers to the distribution of this species along the far eastern region of mainland Asia.

3.4. *Trichoclinocera dasyscutellum* (Saigusa)

(Figs. 2, 3, 7, 13, 18-20, 23)

Acanthoclinocera dasyscutellum Saigusa, 1965: 54.

Trichoclinocera dasyscutellum: SINCLAIR 1994: 1015.

Type Material. Holotype, male labelled: "[HONSHU]/ Kanayama/ YAMANASHI/ 19.VIII.1962/ T. SAIGUSA" (BLKU).

Paratypes: 2 ♂, 1 ♀, same data as holotype (CNC); 21 ♂, 17 ♀, same data as holotype (BLKU).

Additional Material. (375 specimens) JAPAN: **Akita**: Kuroyu, Hachimantai, 8.vii.1962 (BLKU). Nyntosan, Hachimantai, 9.vii.1962 (BLKU). **Aomori**: Oirase-keikoku nr. Tawadoko, 14.viii.1962 (BLKU). **Gifu**: Futatsuya, Kawai-mura, 11.vi.1977 (BLKU). **Iwate**: Hayachinesan, 800-1000 m, 24.vii.1973 (BLKU); Hatatine, 4.viii.1964 (HUS). **Nagano**: Inakoyu, 14.viii.1975 (BLKU); Inakoyu, Kitayatsugatake, 14.viii.1975 (BLKU); Iwanadome, Shimashima, 13.vii.1963 (BLKU); Tobirakôsen, Utsugushigaharn, 18.vii.1963 (BLKU). **Yamanashi**: Hirogawara, Kitadake, 18-19.viii.1978 (BLKU); Kanayama, Kinpusan, 1.vii.1963 (BLKU); Kanayama, Sudama, 10-11.viii.1961, 6.vii.1962, 30.vi., 24.viii.1963, 12-13.viii.1973, 20,30.vi., 2-31.viii., 1,16.ix.1975 (BLKU); Kanayama, Kanayamotôge, 2.vii.1963 (BLKU); Motodanigawa, Kanayama, 9.vii.1975 (BLKU); Tokusatôge, Sudama, 23.vi.1975 (BLKU). Several specimens deposited in BMNH and ZFMK.

Recognition. This species is readily distinguished from other species of the *T. dasyscutellum* group by the reddish-brown coloured legs, long dorsocentral bristles and spur-like bristle on the hind tibia.

Description. Wing length 3.6-4.2 mm.

Male. Dark brown to black in ground colour. Head rounded; compound eye large, rounded. Face narrowest at middle, ca. width of antennal sockets, with pale blue pruinescence, lower margin of face nearly straight, lacking pronounced carina or notch (Fig. 19); width of gena one-sixth height of eye. Ocellar bristles longest among cranial bristles; occiput with 3 pairs of bristles posterior to ocellar triangle; postocular with row of short bristles along margin of eye, upper 3-4 bristles darker and more stout than lower bristles. Arista-like stylus long and slender, tapered apically. Palpus slender, length less than one-half height of eye.

Pleura entirely clothed in blue pruinescence; posterolateral corner of scutum near postalar ridge pale brown. Thoracic bristles long, some longer than width of eye; several acr anterior to first dc; 5-6 pairs dc; 1 pprn; 1 presut spal; 2 npl; 2 psut spal; 1 pal; 2 pairs sctl and numerous pale setulae on disc; several pale bristles on notopleural depression. Laterotergite with patch of pale bristles; prothoracic episternum, katepisternum, and hind margins of metepisternum with long, pale hairs.

Wing (Fig. 13) narrow, infuscate; narrow, faint, parallel-sided stigma present. One long, basal costal bristle, subequal to length of posterior dc; often 1 proximal costal bristle, shorter than one-half length of basal bristle. Row of setulae from base of R to tip of R_1; cell dm strongly produced apically; R_4 and R_5 slightly divergent. Halter brown with pale base.

Legs reddish-brown, darker toward apex. Coxae with long pale, marginal hairs; mid and hind coxae with tinge of pale pruinescence. Fore femur with 4-5 slender anterior bristles on apical third, dorsal to spine-like bristles (Fig. 23); antero- and posteroventral row of long, pale slender bristles along entire length, slightly longer than width of femur; 4-5 black, spine-like anteroventral bristles on apical fourth; anterodorsal region with row of short, stout, black bristles on basal third. Fore tibia with anteroventral row of short, stout bristles and posteroventral row of slender bristles. Mid femur with pair of black, spine-like antero- and posteroventral preapical bristles, longer and more slender than corresponding bristles of fore femur; lacking erect antero- and posterodorsal bristles. Hind femur with 1-2 stout anteroventral preapical bristles, similar to mid femur; lacking antero- and posterodorsal bristles. Hind tibia with posterodorsal spur-like bristle one-third from base, slightly longer than width of tibia; 2-3 posterodorsal preapical spine-like bristles, longer than width of tibia. Tarsi longer than corresponding tibiae. Empodium pulvilliform, subequal in length to claw, less than one-half length of tarsomere.

Hypandrium (Fig. 2) long and cylindrical, longer than epandrium. Phallus long, distinctly bent sub-basally; apex with cup-shaped process; ejaculatory apodeme gently recurved anteriorly. Surstylus very slender, somewhat twisted and arched medially, with membranous oval scolex-like apex. Clasping cercus slender, finger-like, bearing stout bristles on inner dorsal margin.

Female. Similar to male except as follows: fore tibia lacking modified bristles beneath. Terminalia: sclerites of segment 8 narrowly separated laterally; T8 with posterior row of long bristles, subequal to length of sclerite (Fig. 3); T10 with stout, curved bristles along inner and posterior margins, with 3-4 apical bristles more stout than remaining bristles; anteroventral corner of T10 not strongly narrowed and prolonged.

Geographical Distribution and Seasonal Occurrence. This species is restricted to the Japanese island of Honshu (Fig. 7), with flight records from mid-June to mid-September.

Remarks. This species was originally assigned to the genus *Acanthoclinocera* Saigusa, but was transferred to *Trichoclinocera* when the former was considered to be congeneric (SINCLAIR 1994). *Trichoclincera dasyscutellum* is most closely related phylogenetically to *T. asiatica* on the basis of the long thoracic bristles and similarities of the clasping cercus and apex of the phallus.

3.5. *Trichoclinocera feuerborni* (Engel) comb. nov.
(Fig. 4)

Clinocera (s.s) *feuerborni* Engel, 1931: 487.

Type Material. Lectotype male (here designated) labelled: "FS 2a. 6/XII"; "Ngatiloga-Fall/ b. Sarangan. M. Java./ 6.XII.28. (Feuerborn.) [hand-written]"; "[red label, no writing]"; "♀ Clin./ Feuerborni n.sp./ det. Engel" (SMNS). A lectotype label "LECTOTYPE/ of Clinocera/ feuerborni Engel/ des. B.J. Sinclair 2004 [red label]" has been attached to this specimen.

Paralectotype: Same data as lectotype, with a yellow paralectotype label attached (1 ♀, SMNS) [abdomen glued to thorax].

ENGEL (1931) writes that the two type specimens were stored in alcohol, but it must have been dried by him subsequently. ENGEL (1931) also described the species *Kowarzia velutina* (also based on two specimens) in the same publication (see Appendix), and given that there were four specimens all bearing red labels (without writing) stored together under the label *Clinocera feuerborni*, it appears that the type material of these two species were subsequently mixed. Consequently lectotypes are designated for both species at this time to clearly distinguish the type material of these two species.

Recognition. This species is distinguished from other species of the *T. dasyscutellum* group by its brown ground colour and long bristles on the radial vein.

Description. Wing length 4.0-4.1 mm.

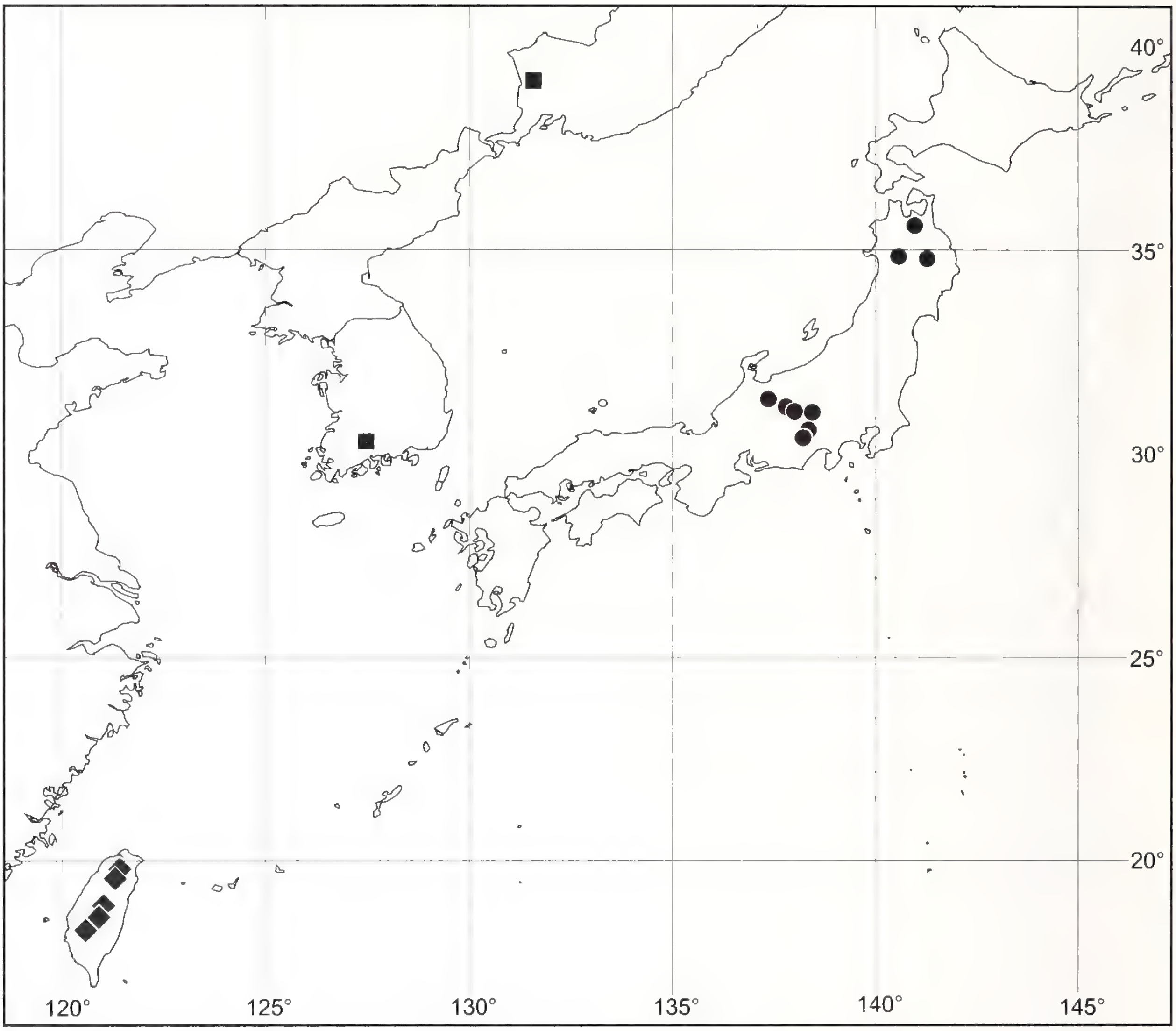


Fig. 7: Known distribution of species of *Trichoclinocera dasyscutellum* group. *T. asiatica* sp. nov. (■), *T. dasyscutellum* (Saigusa) (●), *T. taiwanensis* sp. nov. (◆).

Male. Dark brown in ground colour. Head rounded; compound eyes large, rounded. Face narrowest at middle, ca. width of antennal sockets, with pale blue pruinescence on lower half, lower margin of face with slightly pronounced carina or notch; width of gena one-fifth height of eye. Ocellar bristles longest among cranial bristles; occiput with 3 pairs of bristles posterior to ocellar triangle; postocular with row of short bristles along margin of eye, upper 3-4 bristles darker and more stout than lower bristles. Arista-like stylus long and slender, only slightly tapered apically. Palpus slender, length less than one-half height of eye.

Pleura, postpronotal lobe and notopleural depression entirely clothed in pale blue pruinescence. Thoracic bristles well developed, all shorter than width of eye; acr absent; 5 pairs dc; 1 pprn; 1 presut spal; 2 npl; 2 psut spal; 1 pal; 2 pairs sctl and numerous setulae on disc; several pale bristles on notopleural depression. Laterotergite with patch of pale bristles; prothoracic episternum, katepisternum, and hind margins of metepisternum lacking long pale hairs.

Wing narrow, infuscate; narrow, faint, parallel-sided stigma present. One long, basal costal bristle, subequal to length of sctl. Row of setulae from base of R to tip of R_1, with 3-5 outstanding bristles proximal to origin of Rs ca. one-half length of basal costal bristle; cell dm long, strongly produced apically; R_4 and R_5 very slightly divergent. Halter brown with pale base.

Legs pale brown, darker toward apex. Coxae with long pale, marginal hairs; mid and hind coxae with tinge of pale pruinescence. Fore femur lacking anterior bristles and spine-like bristles; antero- and posteroventral margins with row of long, pale slender bristles along entire length, shorter than width of femur; posteroventral base with 1 long bristle, ca. twice width of femur. Fore tibia with antero- and posteroventral row of short stout bristles. Mid femur lacking spine-like preapical bristles, all outstanding erect bristles lacking, except several slender preapical anteroventral bristles. Hind femur with 1-2 slender anteroventral preapical bristles, similar to mid femur; lacking antero- and posterodorsal bristles. Hind tibia lacking posterodorsal spur-like bristle; 2-3 erect anteroventral preapical bristles, longer than width of tibia. Tarsi longer than corresponding tibiae. Empodium pulvilliform, subequal in length to claw, less than one-half length of tarsomere.

Hypandrium (Fig. 4) long and cylindrical, longer than epandrium. Phallus long, distinctly bent sub-basally; apex with narrow lateral membranous ridges; ejaculatory apodeme gently recurved anteriorly. Surstylus tapered, with narrow membranous scolex-like apex. Clasping cercus strongly arched at base, finger-like, tapered apically, lacking stout bristles on inner margin.

Female. Similar to male except as follows: ventral bristles of fore femur not as numerous; apical fourth with 6-8 spine-like anteroventral spine-like bristles; fore tibia lacking modified bristles beneath. Terminalia (not dissected): sclerites of segment 8 narrowly separated laterally; T8 with posterior row of long bristles. T10 with stout curved bristles along inner and posterior margins.

Geographical Distribution and Seasonal Occurrence. This is the first known occurrence of this genus from Indonesia. The type specimens were collected at a waterfalls in middle Java (ENGEL 1931).

Remarks: This species was listed under *Clinocera* Meigen (unplaced to species-group) by SINCLAIR (1995), but syntypes had not been examined.

3.6. *Trichoclinocera fluviatilis* (Brunetti)

(Figs. 5, 12, 14, 24)

Clinocera fluviatilis Brunetti, 1913: 34.

Trichoclinocera fluviatilis: SINCLAIR 1994: 1016.

T. fluviatilis: WAGNER et al. 2004: 25.

Type Material Examined. Holotype, male labelled: "Clinocera/ fluviatilis/ Brun. Typ ♂" [hand written]; "[India; Uttar Pradesh] NEAR BHOWALI,/ KUMAON: 5,700 FT/ A.D. IMMS 1910/ 12th June. On stones in stream"; "Clinocera fluviatilis/ m ♂" [hand written]; "TYPE"; "1422/ HI" [terminalia partially damaged, only midlegs remain] (ZSI).

Additional Material. (101 specimens) CHINA: **Yunnan:** Dali, Daboping, 1900-2200 m, 7kmW Xiaguan, 16.viii.1995 (BLKU); Jingping, Taiyangzhai, 1500-1600 m, 27.v.1996 (BLKU); Pingbian, Xinxinghe, 780 m, S Pingbian, 3.iii.1995 (BLKU). INDIA: **Himachal Pradesh:** Punj-pul Nullah, Dalhousie, 6500', 8.v.1927 (BMNH). NEPAL: Chiliwa, 1350 m, 27° 29'N, 87 47'E, Shibku, 2100m, 27° 30'N, 87° 41'E, 7.vi.1972 (BLKU); Handhurung, 800 m, 27° 23'N, 87° 40'E, Linba, 1200 m, 27° 24'N, 87° 38'E, 27.vi.1972 (BLKU); Jilikinpthi, 1850 m, 27° 09'N, 87° 30'E, Pontak, 1800 m, 27° 13'N, 87° 33'E, 13.v.1972 (BLKU); Kathmandu, Godavari, 6000', 22.vii.1967 (CNC); Lelep, 1770 m, 27 31'N, 87° 47'E, 1-4.vi.1972 (BLKU); Lelep, 1770 m, 27 31'N, 87° 47'E, Chiliwa, 1350 m, 27° 29'N, 87° 47'E, 7.vi.1972 (BLKU); Methirum, 1000 m, 27° 24'N, 87 42'E, Tiwa, 1400 m, 27° 29'N, 87° 46'E, 29.v.1972 (BLKU); Naudhara - Bhadaue, nr. Pokhara, 1400-1600 m, 9.xi.1971 (BLKU); Shibku, 2100 m, 27° 30'N, 87° 41'E, Shawa, 2300 m, 27° 29'N, 87° 39'E, 8.vi.1972 (BLKU); Siwapuri, 1640 m, 22.v.1981 (BLKU). Several specimens deposited in ZFMK.

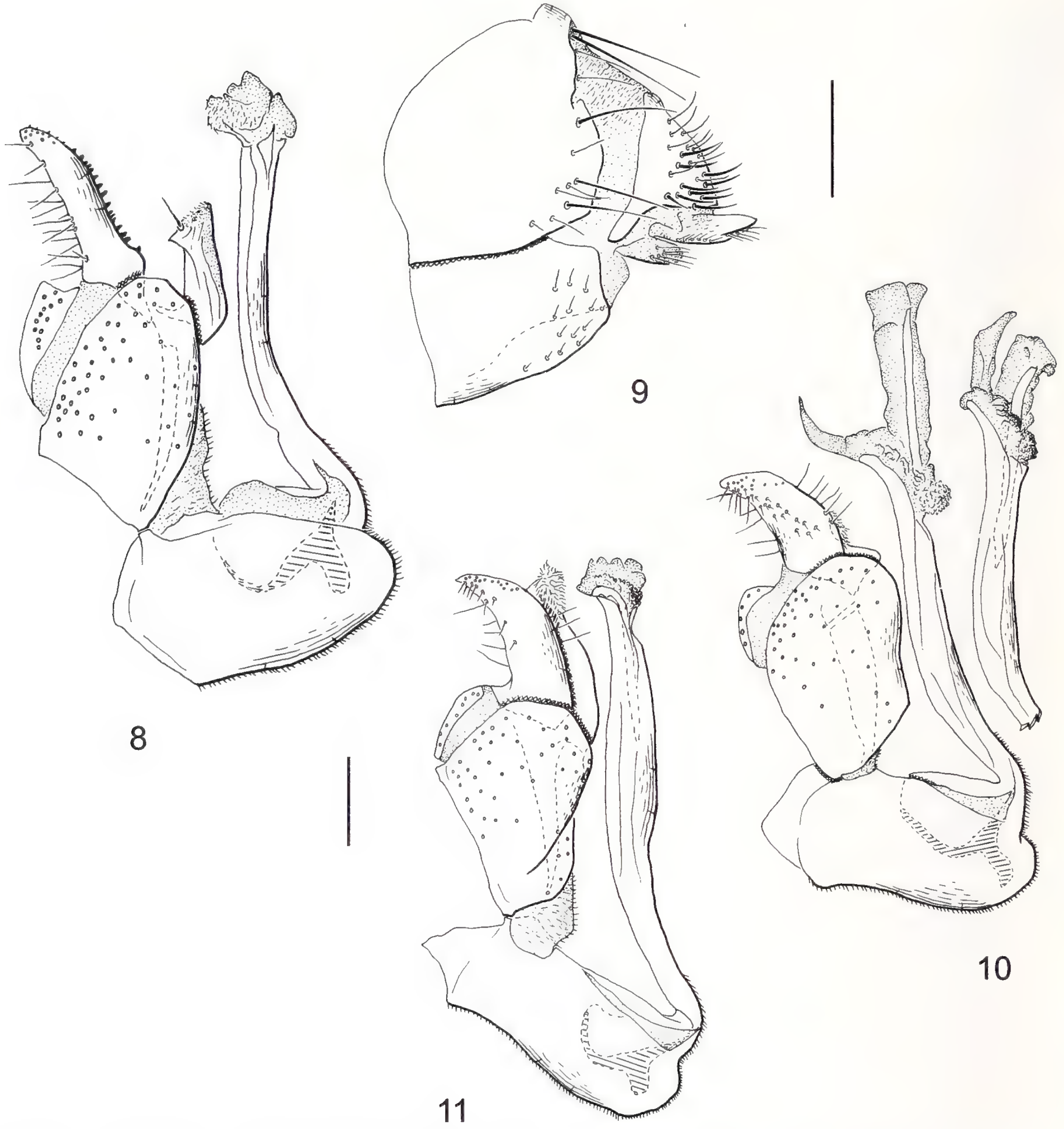
Recognition. This species is distinguished from other species of the *T. dasyscutellum* group by its blue pruinescence and relatively straight clasping cercus.

Description. Wing length 3.6-4.3 mm.

Male. Dark brown with bright blue pruinescence. Head rounded; compound eye large, rounded. Face narrowest at middle, ca. width of antennal sockets, with bright blue pruinescence, lower margin of face nearly straight, lacking pronounced carina or notch; width of gena one-sixth height of eye. Anterior margin of ocellar triangle pale brown, lower postocciput and gena with blue pruinescence; vertex and upper part of postocciput dark when viewed dorsally. Ocellar bristles longest among cranial bristles; occiput with 3 pairs of bristles posterior to ocellar triangle; postocular with row of short bristles along margin of eye, upper 3-4 bristles dark, stouter than lower bristles. Arista-like stylus long and slender, slightly tapered apically. Palpus somewhat clavate, length less than one-half height of eye.

Pleura, postpronotal lobe, notopleuron entirely clothed in bright blue pruinescence; posterolateral corner of scutum including postalar ridge pale brown. Thoracic bristles short, shorter than one-half width of eye; acr lacking; 5 pairs slender dc; 1 slender pprn; 1 presut spal; 2 stout npl; 2 psut spal; 1 very short, slender pal; 2 pairs sctl and several dark marginal setulae; several pale setulae on notopleural depression. Laterotergite with patch of pale bristles; prothoracic episternum with pale hairs; katepisternum and hind margins of metepisternum lacking hairs.

Wing (Fig. 14) narrow, infuscate; narrow, faint, elliptical, stigma present. One basal costal bristle, nearly twice length of posterior dc. Row of setulae from base of R to tip of R_1; cell dm strongly produced apically; R_4



Figs. 8-11: Terminalia of *Trichoclinocera dasyscutellum* group. (8) *T. nepalensis* sp. nov., male; (9) *T. taiwanensis* sp. nov., female; (10) *T. taiwanensis* sp. nov., male with phallus partially and totally extended; (11) *T. yunnana* sp. nov., male with inner apical rod retracted. Scale bar = 0.1 mm.

and R_5 somewhat divergent apically. Halter knob dark with pale shaft.

Legs entirely dark; coxae with bright blue pruinescence. Coxae with long golden marginal hairs. Fore femur with 1 black, spur-like anteroventral bristle on apical fifth (Fig. 24); lacking anterior bristles on apical third, dorsal to spine-like bristles; anteroventral row of short, pale bristles, shorter than one-third width of femur; posteroventral row of slender, pale bristles longer than anteroventral bristles, with 1 basal bristle longer than width of femur; anterodorsal region lacking row of stout bristles on basal third. Fore tibia with biserial row of short stout bristles beneath. Mid femur with 1 black, spur-like anteroventral preapical bristle, slightly shorter than width of femur, similar in size to anteroventral bristle of fore femur; lacking erect antero- and posterodorsal bristles. Hind femur with 1 anteroventral preapical bristle, subequal to width of femur, much more slender than preapical bristle of mid femur; lacking antero- and posterodorsal bristles. Hind tibia lacking posterodorsal spur-like bristle near base; 2 ventral preapical bristles, longer than width of tibia. Tarsi longer than corresponding tibiae. Empodium pulvilliform, subequal in length to claw, less than one-half length of tarsomere.

Hypandrium (Fig. 5) cylindrical, broad, longer than epandrium. Phallus short, strongly curved sub-basally; anterior margin of apex slightly curved, lacking membranous sac; posterior margin of apex with rounded, membranous lobes; ejaculatory apodeme sharply recurved anteriorly. Surstylus sharply produced posteriorly, gun-shaped, with membranous oval scolex-like apex. Clasping cercus straight, projected obliquely, finger-like, strongly tapered to narrow apex, bearing stout anteroventral bristles on outer face; inner margin with long bristles, lacking peg-like bristles.

Female. Similar to male except as follows: fore femur with 2-3 spur-like bristles, apical 2 bristles subequal to width of femur; biserial row of bristles beneath not as dense and distinctive as male; fore tibia lacking modified bristles beneath. Terminalia very similar to *T. taiwanensis*: sclerites of segment 8 overlap laterally; T8 with sparse posterior row of long and short bristles, dorsal bristles nearly subequal to length of sclerite; T10 with stout, curved bristles on apical two-thirds, with apical bristles more stout than remaining bristles; anteroventral corner of T10 narrowed and prolonged obliquely.

Geographical Distribution and Seasonal Occurrence. This species ranges from Northern India and Nepal, eastward to Yunnan (Fig. 12). In Nepal it ranges from 1000-2000 m, sympatric with *T. nepalensis*.

3.7. *Trichoclinocera naumanni* sp. nov. (Figs. 6, 12)

Type Material. Holotype, male labelled: "[CHINA: Sichuan]/ Maziba, 1100-/ 1300 m, Emeishan/ Aug. 16, 1998/ T. SAIGUSA col." (BLKU).

Paratypes: CHINA: **Sichuan:** 4 ♂, 8 ♀, same data as holotype (BLKU, ZFMK).

Recognition. Distinguished by its brownish integument, especially the pale brown coxae and arched and strongly tapered clasping cercus.

Description. Wing length 3.6-4.0 mm.

Male. Dark brown with brownish-orange markings and faint blue pruinescence. Head rounded; compound eye large, rounded. Face narrowest at middle, ca. width of antennal sockets, with pale whitish pruinescence on lower third; lower margin of face with slight cleft with small carina or swelling; width of gena one-sixth height of eye. Vertex and ocellar triangle dark brown, lower postocciput and gena slightly pruinescent. Ocellar bristles longest among cranial bristles; occiput with 3 pairs of bristles posterior to ocellar triangle; postocular with row of short bristles along margin of eye, upper 3-4 bristles dark, stouter than lower bristles. Arista-like stylus long and slender, not tapered apically. Palpus somewhat clavate, length less than one-third height of eye.

Pleura brown with pale areas along sutures, with tinge of pale blue pruinescence when viewed from above; postpronotal lobe, notopleuron, posterior half of anepimeron pale brown and posterolateral corner of scutum including postalar ridge pale brown. Thoracic bristles short, less than one-half width of eye; acr lacking; 5 pairs slender dc; 1 slender short pprn, one-third to one-half length of dc; 1 presut spal; 2 stout npl; 2 psut spal; 1 very short, slender pal; 2 pairs sctl and several pale setulae laterally; several pale setulae on notopleural depression. Laterotergite with small patch of dark bristles; prothoracic episternum with pale hairs; katepisternum and hind margins of metepisternum lacking hairs or very scarce.

Wing narrow, infuscate; narrow, faint, elliptical, stigma present. One basal costal bristle, nearly twice length of posterior dc. Row of setulae from base of R to tip of R_1; cell dm produced apically; R_4 and R_5 divergent. Halter knob dark with pale shaft.

Legs dark brown, except inner base of mid femur and base of hind femur pale; coxae brownish orange, darker on anterior margin of fore coxa; lacking blue pruinescence. Coxae with long dark marginal hairs. Fore femur with 2 black, spur-like anteroventral subapical bristles; lacking anterior bristles on apical third, dorsal to spine-like bristles; anteroventral row of short, pale bristles, ca. one-half width of femur; posteroventral row of slender, pale bristles with basal bristles nearly subequal to width of femur, with 1 basal bristle twice width of femur. Fore tibia with biserial row of short, stout bristles beneath. Mid femur with 1 black, spur-like anteroventral preapical bristle, subequal to width of femur, similar in size to anteroventral bristles of fore femur; lacking erect antero- and posterodorsal bristles. Hind femur with 1 slender anteroventral preapical bristle, subequal to width of femur, much more slender than preapical bristle of mid femur; lacking antero- and posterodorsal bristles. Hind tibia lacking posterodorsal spur-like bristle near base; 2 ventral erect bristles, longer than width of tibia on apical fifth; 1-2 erect, preapical dorsal bristles. Tarsi longer than corresponding tibiae. Empodium pulvilliform, subequal in length to claw, ca. one-half length of tarsomere.

Hypandrium (Fig. 6) cylindrical, distinctly longer than epandrium; anterior margin produced into broad apodeme. Phallus not extending beyond clasping cercus;

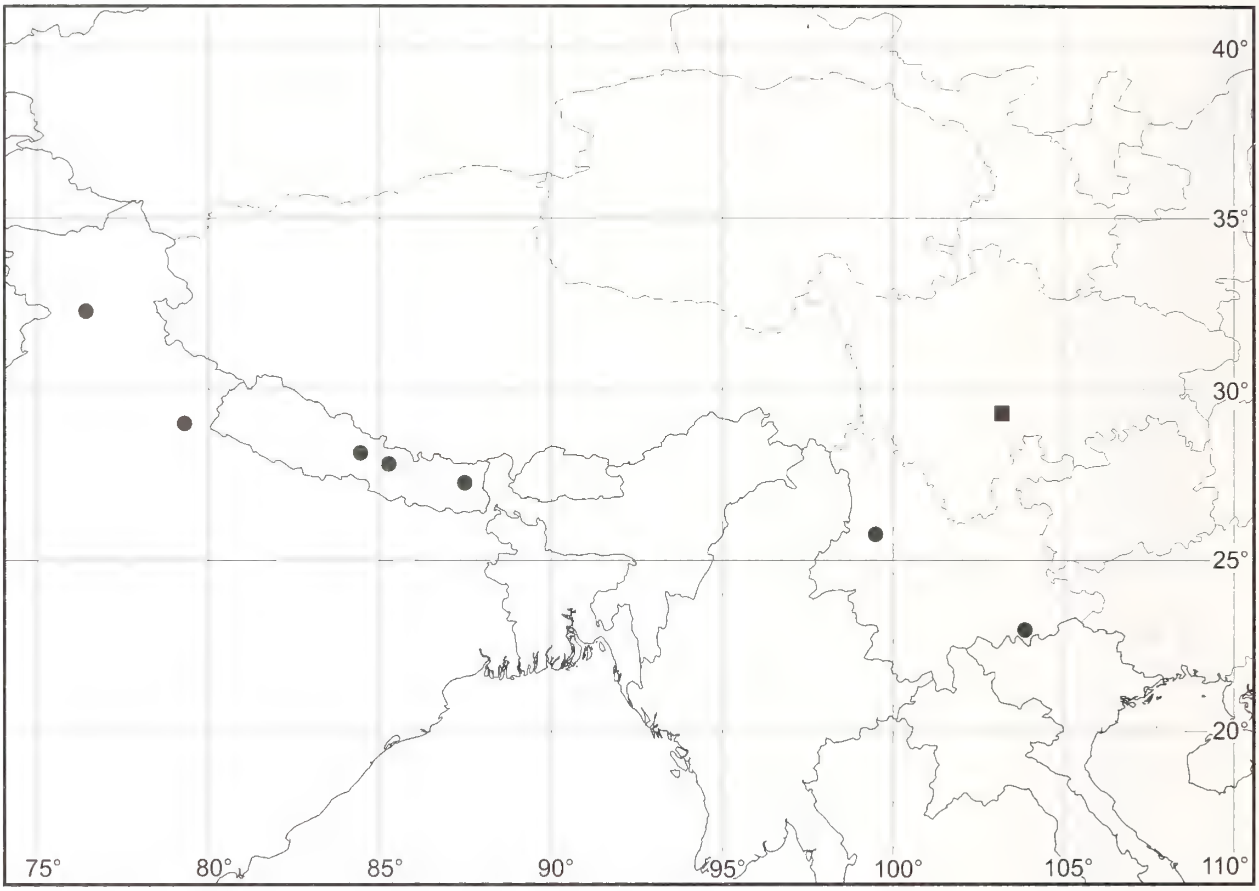


Fig. 12: Known distribution of species of *Trichoclinocera dasyscutellum* group. *T. fluviatilis* (Brunetti) (●), *T. naumanni* sp. nov. (■).

somewhat curved sub-basally; anterior margin of apex curved, with short membranous sac; posterior margin of apex with rounded pair of lobes, clothed in microtrichia; long, straight rod with membranous sheath projected apically, nearly one-third length of phallic shaft, often partially or completed retracted within shaft of phallus; ejaculatory apodeme arched strongly anteriorly. Surstylus slender, subequal in length to clasping cercus with angular base, partially arched subapically, with membranous cylindrical scolex-like apex. Clasping cercus strongly curved, claw-like, strongly tapered to narrow apex, bearing short bristles on outer face, concentrated near apex; inner margin with short slender bristles.

Female. Similar to male except as follows: fore femur with 3-4 preapical, anteroventral spur-like bristles; biserial row of bristles beneath not as dense and distinctive as male; fore tibia lacking modified bristles beneath. Terminalia similar to *T. taiwanensis*.

Geographical Distribution and Seasonal Occurrence. This species is currently known only from the Sichuan Province of China (Fig. 12).

Remarks. This species is most closely related to *T. yunnana*, on the basis of their very similarly shaped clasping cercus and configuration of the membranous apex of the phallus.

Etymology. The specific name honours the late Dr. Clas M. NAUMANN, in recognition of his dedication to entomology, systematics and Museum Koenig.

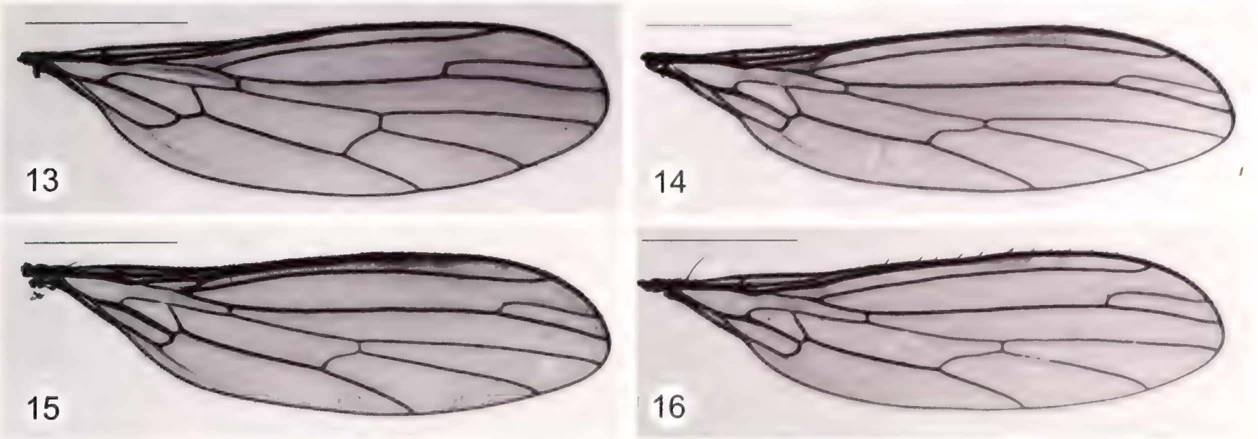
3.8. *Trichoclinocera nepalensis* sp. nov.

(Figs. 8, 15, 17, 25)

Type Material. Holotype, male labelled: "NEPAL, Ktmd./ Godavari 6000'/ 18 July 1967/ Can. Nepal Exped." (CNC).

Paratypes: NEPAL: 10 ♂, 5 ♀, same data as holotype (CNC); 8 ♂, 14 ♀, 22.vii.1967, same locality as holotype (CNC); 5 ♂, 17 ♀, Lelep, 1770 m, 27° 31'N, 87° 47'E, 1-4.vi.1972, JE/ HS (BLKU); 1 ♀, Pulchauk, 6600', 21.vii.1967, Can. Nepal Exped. (CNC); 2 ♂, Takwa, 1500 m, 27° 31'N, 87° 48'E, Lelep, 1770 m, 27° 31'N, 87° 47'E, 1.vi.1972, HS (BLKU). VIETNAM: 12 ♂, 22 ♀, Lao Cai Prov., Sa Pa, 1600 m, 27.v.1997, RM (BLKU). Several specimens deposited in ZFMK.

Recognition. Distinguished from other Nepalese species by lacking distinctive blue pruinescence, straight



Figs. 13-16: Wings of *Trichoclinocera dasyscutellum* group. (13) *T. dasyscutellum* (Saigusa); (14) *T. fluviatilis* (Brunetti); (15) *T nepalensis* sp. nov.; (16) *T. yunnana* sp. nov. Scale bar = 1.0 mm.

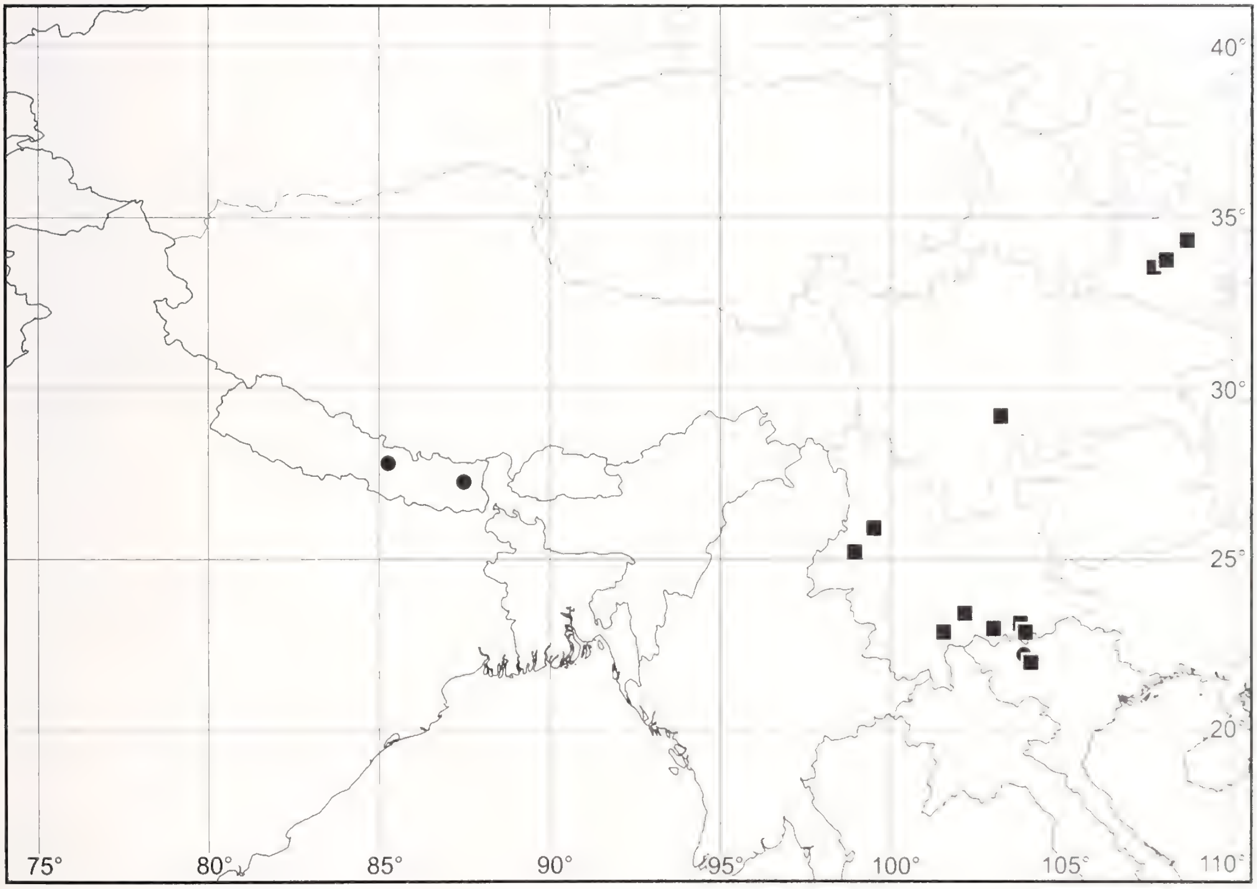


Fig. 17: Known distribution of species of *Trichoclinocera dasyscutellum* group. *T. nepalensis* sp. nov. (●), *T. yunnana* sp. nov. (■).

clasping cercus and surstylus bearing a stout, apical bristle.

Description. Wing length 3.6-4.3 mm.

Male. Dark brown with brownish-orange markings and faint blue pruinescence. Head rounded; compound eye large, rounded. Face narrowest at middle, ca. width of antennal sockets, with pale whitish pruinescence on lower half; lower margin of face with slight cleft with small carina or swelling; width of gena one-sixth height of eye. Vertex and ocellar triangle dark brown, lower postocciput and gena slightly pruinescent. Ocellar bristles longest among cranial bristles; occiput with 3 pairs of bristles posterior to ocellar triangle; postocular with row of short bristles along margin of eye, upper 3-4 bristles dark, stouter than lower bristles. Arista-like style long and slender, slightly tapered apically. Palpus somewhat clavate, length less than one-third height of eye.

Pleura brown with tinge of pale blue pruinescence; postpronotal lobe, notopleuron, posterior half of anepimeron pale brown and posterolateral corner of scutum including postalar ridge pale brown. Thoracic bristles short, less than one-half width of eye; acr lacking; 5 pairs slender dc; 1 slender short pprn, one-fourth length of dc; 1 presut spal; 2 stout npl; 2 psut spal; 1 very short, slender pal; 2 pairs sctl and several pale setulae laterally; several pale setulae on notopleural depression. Laterotergite with patch of dark bristles; prothoracic episternum with pale hairs; katepisternum and hind margins of metepisternum lacking hairs or very scarce.

Wing (Fig. 15) narrow, infuscate; narrow, faint, elliptical, stigma present. One basal costal bristle, nearly twice length of posterior dc. Row of setulae from base of R to tip of R_1; cell dm produced apically; R_4 and R_5 somewhat divergent apically. Halter knob dark with pale shaft.

Legs dark brown, except inner base of hind femur pale; coxae brownish orange, darker on anterior margin, especially fore coxa; lacking blue pruinescence. Coxae with long dark marginal hairs. Fore femur with 1 black, spur-like anteroventral subapical bristle (Fig. 25); lacking anterior bristles on apical third, dorsal to spine-like bristles; anteroventral row of short, pale bristles, ca. one-half width of femur, with 1 basal bristle nearly twice width of femur; posteroventral row of slender, pale bristles similar to anteroventral bristles, with 1 basal bristle twice width of femur; anterodorsal region with row of very short, reduced bristles on basal third. Fore tibia with biserial row of short stout bristles beneath. Mid femur with 1 black, spur-like anteroventral preapical bristle, subequal to width of femur, similar in size to anteroventral bristle of fore femur; lacking erect antero- and posterodorsal bristles. Hind femur with 1 slender anteroventral preapical bristle, shorter than width of femur, much more slender than preapical bristle of mid femur; lacking antero- and posterodorsal bristles. Hind tibia lacking posterodorsal spur-like bristle near base; 2 ventral erect bristles, longer than width of tibia on apical fifth; 1 erect, preapical dorsal bristle. Tarsi longer than corresponding tibiae. Empodium pulvilliform, subequal in length to claw, ca. one-half length of tarsomere.

Hypandrium (Fig. 8) oval, more broad anteriorly, slightly longer than epandrium. Phallus short, shallowly curved sub-basally; anterior margin of apex curved, with short membranous lobe clothed in microtrichia; posterior margin of apex with rounded membranous lobes; ejaculatory apodeme gradually recurved anteriorly. Surstylus ca. one-half length of clasping cercus, sharply produced anteroapically, with membranous posterior and apical margin clothed with short microtrichia; apex bearing long bristle mounted on cylindrical process. Clasping cercus straight, finger-like, gradually tapered to rounded apex, bearing slender anteroventral bristles on outer face; inner margin with short, stout, peg-like bristles.

Female. Similar to male except as follows: fore femur with 0-3 stout anteroventral bristles basal to preapical spine-like bristle; biserial row of bristles beneath not as dense and distinctive as male; fore tibia lacking modified bristles beneath. Terminalia very similar to *T. taiwanensis*: sclerites of segment 8 partially overlap laterally; T8 with sparse posterior row of long and short bristles, dorsal bristles nearly subequal to length of sclerite; T10 with stout, curved bristles on apical two-thirds, with apical bristles more stout than remaining bristles; anteroventral corner of T10 narrowed and prolonged obliquely.

Geographical Distribution and Seasonal Occurrence. This species is known from Nepal and northern Vietnam (Fig. 17) and is sympatric with *T. fluviatilis* in Nepal and *T. yunnana* in Vietnam.

Remarks. The clasping cercus of the Vietnam population is more straight compared to the Nepalese population which is slightly arched apically.

Etymology. The specific name refers to the type locality and where the majority of the specimens were collected.

3.9. *Trichoclinocera taiwanensis* sp. nov.

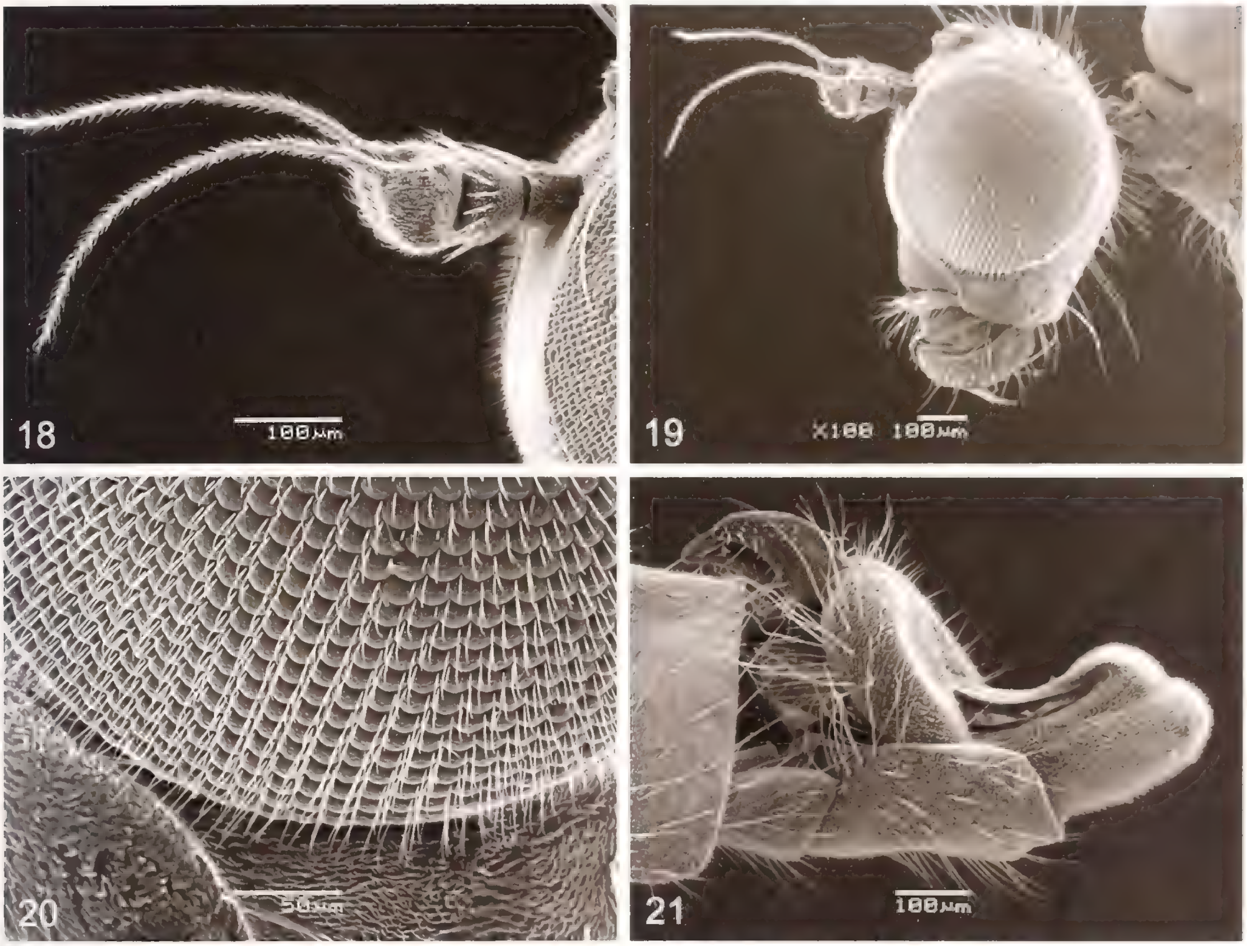
(Figs. 7, 9, 10, 21, 26)

Type Material. Holotype male labelled: "(Taiwan)/ Wulai/ Taipei Hsien"; "17.iv.1965/ T. Saigusa" (BLKU).

Paratypes: TAIWAN: **Chiayi-hs.:** 2 ♂, Chiaoliping, 14.iv.1965, TS (BLKU). **Nantou-hs.:** 3 ♀, Tungyenchi, 950 m, Meichi, Jenai-hsiang, 19.xi.1997, BJS (CNC). **Taichung-hs.:** 32 ♂, 37 ♀, Suchilanchi, 1600 m, Huanshan, nr. Lishan, 24-25.xi.1997, river, BJS (ZFMK). **Taipei-hs.:** 26 ♂, 16 ♀, same data as holotype (BLKU); 1 ♂, 1 ♀, Wulai, 31.iii.1984, K. Ohara (BLKU); 16 ♂, 32 ♀, Fushan, Wulai-hsiang, 400-600 m, 28.xi.1997, river, BJS (CNC, ZFMK); 1 ♂, 2 ♀, Han Hsien, Fushan, LTER Site, small river No. 8, 27.iii.2003, L. Papp (HNHM).

Recognition. This species is readily distinguished by the slender pointed anteroapical lobe of the phallus and dull coloured stalks of the halteres.

Description. Wing length 4.5-5 mm.



Figs. 18-21: Scanning electron photographs of *Trichoclinocera*. spp. (18) *T. dasyscutellum* (Saigusa), antennae; (19) *T. dasyscutellum* (Saigusa), compound eye; (20) *T. dasyscutellum* (Saigusa), compound eye and ommatrichia; (21) *T. taiwanensis* sp. nov., male terminalia, lateral view.

Male. Dark brown with distinct blue pruinescence. Head rounded; compound eye large, rounded. Face narrowest at middle, ca. width of antennal sockets, with distinct blue pruinescence, lower margin of face nearly straight, lacking pronounced carina or notch; width of gena one-sixth height of eye. Ocellar bristles longest among cranial bristles; occiput with 3 pairs of bristles posterior to ocellar triangle; postocular with row of short bristles along margin of eye, bristles of upper half to third of eye dark, stouter than lower bristles. Arista-like stylus long and slender, slightly tapered apically. Palpus somewhat clavate, length less than one-half height of eye.

Pleura, postpronotal lobe and notopleuron entirely clothed in bright blue pruinescence; posterolateral corner of scutum including postalar ridge pale blue. Thoracic bristles short, nearly one-half width of eye; acr lacking; 5 pairs dc; 1 pprn; 1 presut spal; 2 npl; 2 psut spal; 1 very short, slender pal; 2 pairs sctl and numerous dark setulae on disc; several pale bristles on notopleural depression. Laterotergite with patch of pale bristles; prothoracic episternum, katepisternum, and hind margins of metepisternum with pale hairs.

Wing narrow, infuscate; narrow, faint, parallel-sided stigma present. One short, basal costal bristle, subequal to length of posterior dc. Row of setulae from base of R to tip of R_1; cell dm strongly produced apically; R_4 and R_5 parallel-sided. Halter dark with dull base, not brightly coloured.

Legs dark; coxae with pale blue pruinescence. Coxae with long golden marginal hairs. Fore femur with 3-4 black, spur-like anteroventral bristles on apical fourth (Fig. 26); lacking anterior bristles on apical third, dorsal to spine-like bristles; anteroventral biserial row of short bristles, shorter than half width of femur; posteroventral row of slender bristles subequal to one-half width of femur, 2-3 basal bristles subequal to width of femur; anterodorsal region lacking row of stout bristles on basal third. Fore tibia with biserial row of short, stout bristles beneath. Mid femur with 1 black, spine-like anteroventral preapical bristle, shorter than width of femur, similar to fore femur; lacking erect antero- and posterodorsal bristles. Hind femur with 1 anteroventral preapical bristle, subequal to width of femur, more slender than preapical bristle of mid femur; lacking antero- and posterodorsal bristles. Hind tibia lacking posterodorsal spur-like bristle near base; 2 ventral and 2 dorsal preapical bristles, longer than width of tibia. Tarsi longer than corresponding tibiae. Empodium pulvilliform, subequal in length to claw, less than one-half length of tarsomere.

Hypandrium (Figs. 10, 21) cylindrical, only slightly longer than epandrium. Phallus short, curved subbasally; anterior margin of apex curved, produced into curved, blade-like, membranous tapered sac; posterior margin of apex with rounded pair of roughened lobes, and long, straight rod with membranous sheath projected apically, nearly one-third length of phallic shaft; ejaculatory apodeme straight anteriorly. Surstylus slender, distinctly bent, twisted and arched medially, with membranous oval scolex-like apex. Clasping cercus curved, finger-like, strongly tapered to narrow apex, bearing rows of short bristles on outer face; inner margin with long silky bristles, subequal to width of lobe.

Female. Similar to male except as follows: fore femur with 5-6 spur-like bristles, increasing in length apically, with stout, short bristles intermixed in anteroventral row; fore tibia lacking modified bristles beneath. Terminalia (Fig. 9): sclerites of segment 8 overlap laterally; T8 with sparse posterior row of long and short bristles, dorsal bristles subequal to length of sclerite; T10 with stout, curved bristles on apical two-thirds, with apical bristles more stout than remaining bristles; anteroventral corner of T10 narrowed and prolonged obliquely.

Geographical Distribution and Seasonal Occurrence. This species is restricted to Taiwan (Fig. 7).

Remarks. The apex of the phallus was often found retracted (Fig. 10), where the long apical rod is withdrawn in the shaft of the phallus and the blade-like sac is also not fully inflated. This retractable rod is present in *T. fluviatilis, T. naumanni, T, yunnana* and possibly also *T. feuerborni*. This structure is unique to this subgroup and supports there close phylogenetic relationship.

Etymology. The specific name refers to its geographic distribution.

3.10. *Trichoclinocera yunnana* sp. nov.

(Figs. 11, 16, 17, 27)

Type Material. Holotype, male labelled: "[CHINA: YUNNAN]/ Huanglianshan/ 1800m, nr. Sanmeng/ Luchun, 9 Mar.1995/ T. SAIGUSA col." (BLKU).

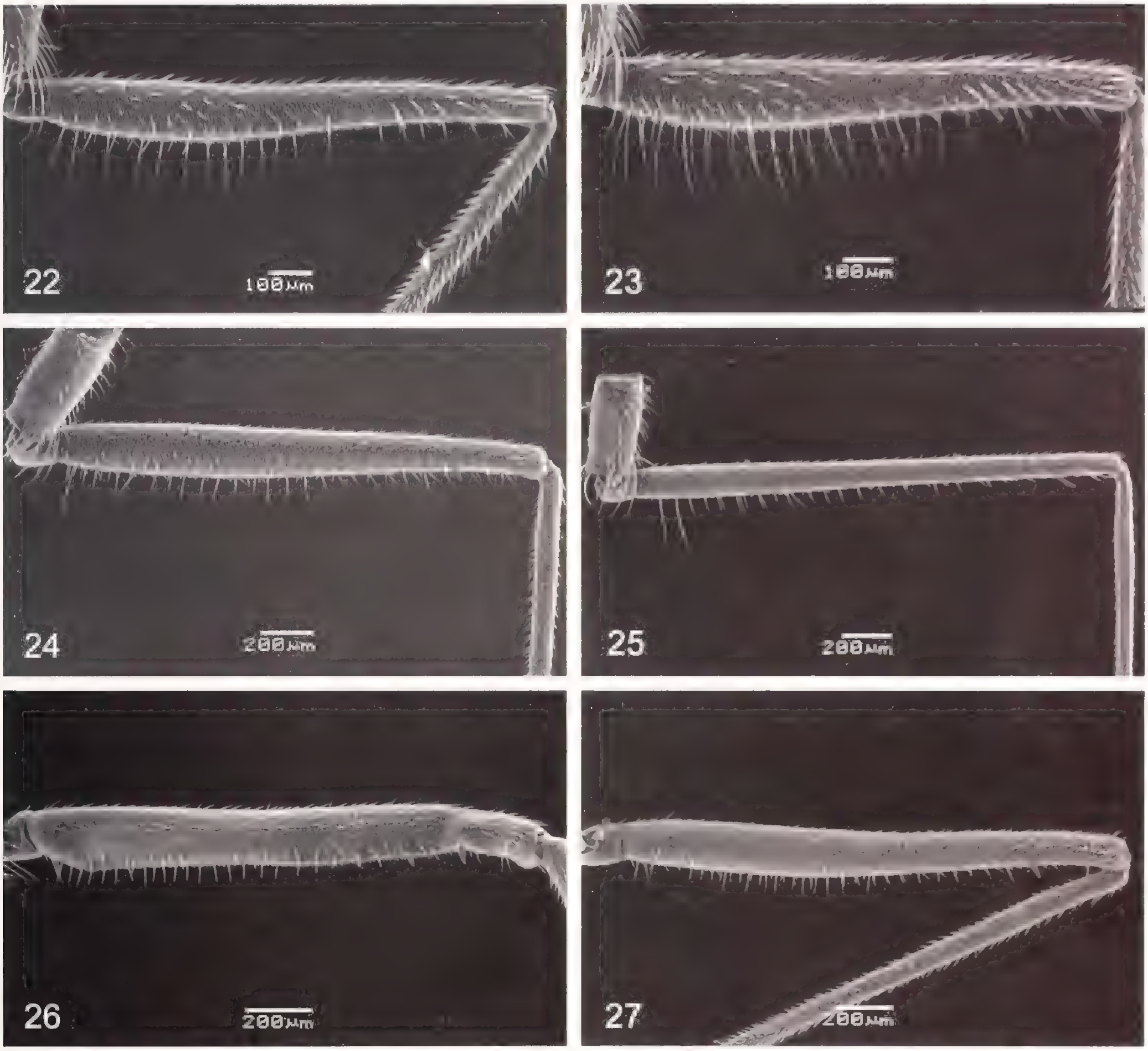
Paratypes: CHINA: **Shaanxi:** 1 ♂, 1 ♀, Fuping-x, Lianfengya, 2000-2100 m, 12 kmWNW, Longcaoping, 24.vi.1997, TS (BLKU); 6 ♂, 14 ♀, Fuping-x, nr. Longcao, 1310-1400 m, 8 kmN Longcaoping, 27.vi.1997, TS (BLKU); 8 ♂, 3 ♀, Fuping-x, Xigou, 1340-1400 m, 5 kmNW Longcaoping, 27.vi.1997, TS (BLKU); 1 ♂, 1 ♀, Zhouzhi-x, Shuimoping, 1500 m, SSW Banfangzi, 3.vii.1997, TS (BLKU). **Sichuan:** 5 ♂, 10 ♀, Jingshui, 700-750 m, Emeishan, 7.viii.1998, TS (BLKU); 1 ♀, Maziba, 1100-1300 m, Emeishan, 16.viii.1998, TS (BLKU). 1 ♂, 4 ♀, Wuxiangang, 700 m, Emeishan, 14.viii.1998, TS (BLKU). **Yunnan:** 36 ♂, 56 ♀, same data as holotype (BLKU); 19 ♂, 32 ♀, Dali, Daboping, 1900-2200 m, 7 kmW Xianguan, 16.viii.1996, TS (BLKU); 2 ♂, Hekou, 3 km from Laofanzha, 200 m, 1.iii.1995, TS (BLKU); 5 ♂, 1 ♀, Hekou, Nanxi-Quiatou, 200 m, 37 km from Hekon, 28.ii.1995, TS (BLKU); 2 ♂, 1 ♀, Nanxi-Quiatou, 150 m, 27 km from Hekou, 26.ii.1995, TS (BLKU); 42 ♂, 52 ♀, Jingcheng, 28 km from Jiangcheng, 1125 m, 12.iii.1995, TS (BLKU); 1 ♀, Jingping, Fenshuiling Nat. Res. 1850 m, 25.v.1996, TS (BLKU); 2 ♂, 2 ♀, Pingbian, Xinxinghe, 780 m, S. Pingbian, 3.iii.1995, TS (BLKU); 1 ♂, 5 ♀, Yongping, Meihuapu, 2300 m, 83 km from Xiaguan, 4.vi.1996, TS (BLKU). VIETNAM: 1 ♂, 1 ♀, Lao Cai Prov., Sa Pa, 1700 m, 26.v.1997, RM (BLKU); 5 ♂, 12 ♀, Lao Cai Prov., Sa Pa, 1600 m, 27.v.1997, RM (BLKU). Several specimens deposited in ZFMK.

Recognition. This species is distinguished by the orange-brown coloured stalks of the halteres and the strongly arched and tapered clasping cercus.

Description. Wing length 4.3-5.4 mm.

Male. Dark brown with distinct blue pruinescence. Head rounded; compound eye large, rounded. Face narrowest at middle, ca. width of antennal sockets, with distinct blue pruinescence, lower margin of face nearly straight with slight notch; width of gena one-fifth height of eye. Ocellar bristles longest among cranial bristles; occiput with 3 pairs of bristles posterior to ocellar triangle; postocular with row of short bristles along margin of eye, bristles of upper third of eye dark, stouter than lower bristles. Arista-like stylus long and slender, tapered apically. Palpus somewhat clavate, length ca. one-third half height of eye.

Pleura, postpronotal lobe and notopleuron entirely clothed in bright blue pruinescence; posterolateral corner of scutum including postalar ridge pale brown. Thoracic bristles short, less than one-half width of eye; acr lacking; 5 pairs dc; 1 pprn; 1 presut spal; 2 npl; 2 psut spal; 1 very short, slender pal; 2 pairs sctl and numerous pale setulae on disc and margin; several pale bristles on notopleural depression. Laterotergite with patch of long, dark bristles; prothoracic episternum with pale hairs; katepisternum and hind margins of metepisternum lacking hairs.



Figs. 22-27: Scanning electron photographs of male forelegs of *Trichoclinocera* spp., lateral view. (22) *T. asiatica* sp. nov.; (23) *T. dasyscutellum* (Saigusa); (24) *T. fluviatilis* (Brunetti); (25) *T. nepalensis* sp. nov.; (26) *T. taiwanensis* sp. nov.; (27) *T. yunnana* sp. nov.

Wing (Fig. 16) narrow, infuscate; narrow, faint, parallel-sided stigma present. One short, basal costal bristle, longer than length of posterior dc. Row of setulae from base of R to tip of R_1; cell dm strongly produced apically; R_4 and R_5 parallel-sided, except at extreme apex. Halter dark with pale base.

Legs dark, except inner base of hind femur paler; coxae brownish orange, darker on anterior margin, especially fore coxa; some specimens with blue pruinescence. Coxae with long, golden marginal hairs. Fore femur with 1 black, spur-like anteroventral preapical bristle (Fig. 27); lacking anterior bristles on apical third, dorsal to spine-like bristles; anteroventral row of slender bristles, one-half to one-third width of femur; posteroventral row of slender bristles similar to anteroventral row, basal bristles only slightly longer than preceding bristles; anterodorsal region lacking row of stout bristles on basal third. Fore tibia with biserial row of slender bristles beneath, one-half width of tibia. Mid femur with 1 black, spine-like anteroventral preapical bristle, subequal to width of femur, similar to fore femur; lacking antero- and posterodorsal bristles. Hind femur with 1 anteroventral preapical bristle, subequal to width of femur, more slender than preapical bristle of mid femur; lacking antero- and posterodorsal bristles. Hind tibia lacking posterodorsal spur-like bristle near base; 2 ventral and 2 dorsal, erect preapical bristles, longer than width of tibia. Tarsi longer than corresponding tibiae. Empodium pulvilliform, subequal in length to claw, more than one-half length of tarsomere.

Hypandrium (Fig. 11) cylindrical, slightly longer than epandrium; anterior margin produced and pointed. Phallus not extending beyond clasping cercus; somewhat curved sub-basally; anterior margin of apex curved, with short membranous sac; posterior margin of apex with rounded pair of lobes, clothed in microtrichia; long, straight rod with membranous sheath projected apically, nearly one-third length of phallic shaft, often partially or completed retracted within shaft of phallus; ejaculatory apodeme gradually arched anteriorly. Surstylus slender, subequal to length of clasping cercus, partially arched subapically, with membranous oval scolex-like apex. Clasping cercus strongly curved, claw-like, strongly tapered to narrow apex, bearing short bristles on outer face, concentrated near apex; inner margin lacking stout bristles.

Female. Similar to male except as follows: fore femur with 2-6 spine-like bristles, increasing in length apically with bristles of posteroventral margin increasing in length basally; fore tibia lacking modified bristles beneath. Terminalia very similar to *T. taiwanensis*: sclerites of segment 8 partially overlap laterally; T8 with posterior row of long and short bristles, dorsal bristles more dense and nearly subequal to length of sclerite; T10 with stout, curved bristles on apical two-thirds, with apical bristles more stout than remaining bristles; anteroventral corner of T10 narrowed and prolonged obliquely.

Geographical Distribution and Seasonal Occurrence. This species is known from Shaanxi, Yunnan and Sichuan Provinces of China and northern Vietnam (Fig. 17).

Remarks. The population from Shaanxi Province bears stouter bristles on the clasping cercus and the base of the surstylus is more distinctly elbowed.

Etymology. The specific name refers to the region where the majority of specimens were collected, including the type locality.

3.11. *Trichoclinocera sp.*

Material examined. THAILAND: 1 ♀, S. Banna, Nakhon, 108 m, 5-10.v.1958, T.C. MAA (BPBM).

Diagnosis. Coxae and base of hind femur orange-brown, bearing golden bristles. Fore femur with 2 anteroventral spine-like bristles; single, dorsal spur-like seta at base of hind femur. Radial branch very short; M_1 and M_2 arising from cell dm closely approximated.

Remarks. The limited material available of this species prevents providing a full description and formal specific name. On the basis of leg colouration, it is possibly related to *T. asiatica*.

Acknowledgements. We are indebted to the following curators and their respective institutions for the loan or permission to examine material: J. Chainey (BMNH), N.L. Evenhuis (BPBM), J.M. Cumming (CNC), M. Ohara (HUS), M. Földvári, (HNHM), P. Tschorsnig (SMNS) and M. Datta (ZSI). T. Tachi and A. Inoue (BLKU) are thanked for producing the wing photos, assisted with the Japanese regional map and creating the SEMs, I.V. Shamshev (St. Petersburg, Russia) provided helpful interpretations for Russian locality names and B. Huber (ZFMK) kindly gave advice concerning the presentation of the maps. This study was partially funded by a Grant from the Ministry of Education (Japan).

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APPENDIX

***Clinocera velutina* (Engel)**

Kowarzia velutina Engel, 1931: 488.

Clinocera velutina: SINCLAIR 1995: 693

Type Material. Lectotype male (here designated) labelled: "Fy 2C 9/7"; "Tjiborom-Fall/ Tjobodas. W. Java./ 9.VII.29. (Feuerborn.) [hand-written]"; "[red label, no writing]"; [dissected, micro-slide mounted beneath] (SMNS). A lectotype label "LECTOTYPE/ of Kowarzia/ velutina Engel/ des. B.J. Sinclair 2004 [red label]" has been attached to this specimen.

Paralectotype: "Wasserfall.b./ Sarangan. M. Java./ Prof. Feuerborn./ 6.VII.28 [hand-written]"; "[red label, no writing]" (1 ♀, SMNS). A yellow paralectotype label has been attached to this specimen.

Redescription. Wing length 3 mm.

Male. Face with pale blue pruinescence, except upper margin of eye; lateral margins with 2-3 fine, pale setulae; lower third of face flat; vertex, gena and posterior region of head brown. Arista-like stylus long and slender. Postocular bristles dark and stout.

Pleura with pale pruinescence present when viewed from several angles. Scutum with pair of indistinct vittae, separated by reddish-brown median stripe. Several short, pale acr scattered anterior to first dc; 5 dc; 1 pprn very slender and reduced; 2 npl, lower weak and short; 1 psut spal; 1 pal; 2 sctl. Laterotergite with patch of long, dark bristles.

Wing infuscate; stigma at apex of cell sc; 1 short basal costal seta; costal spines present. R_{2+3} and R_{4+5} straight; auxiliary crossvein between R_4 and R_{2+3} absent; R_4 bell-shaped; anal vein indistinct or lacking; cell dm produced apically. Halter dark.

Coxae with pale pruinescence; coxae and femora bright yellowish-brown, tibia and tarsi increasingly becoming darker. Fore coxae with pale hairs. Fore femur with antero- and posteroventral row of short stout bristles on basal two-thirds; anterior preapical comb present; dense white ventral pile lacking. Fore tibia with row of stout bristles beneath. Mid and hind femora lacking preapical bristles. Hind tibia with dorsal and ventral erect bristles on apical third. Fifth tarsomere lacking dorsoapical extension; empodium pale brown laterally.

Terminalia slide-mounted, compressed. Hypandrium broadly triangular. Phallus somewhat straight; phallic filament long, flexible and whip-like. Clasping cercus narrow with rounded tip, with dense bristles on inner anterior face. Surstylus with pointed tip.

Female. Similar to male except as follows: ventral bristles of foreleg less distinct; legs darker, especially femora.

Remarks. The male terminalia is not redrawn as the original illustration of ENGEL (1931) is adequate and it is permanently slide mounted and pinned beneath the specimen. SINCLAIR (1995) assigned this species to the *C. lineata*-group on the basis of the form of the surstylus. The presence of facial setulae is a defining synapomorphy of *Kowarzia*, but they are also present in several Asian species, including *C. velutina* (SINCLAIR 1995).

Bonner zoologische Beiträge	Band 53 (2004)	Heft 1/2	Seiten 211–220	Bonn, Juni 2005

Aphyosemion (Mesoaphyosemion) etsamense (Cyprinodontiformes: Aplocheiloidei: Nothobranchiidae), a New Species from the Monts de Cristal, Northwestern Gabon[1]

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Abstract. *Aphyosemion* (*Mesoaphyosemion*) *etsamense* sp. nov., a species belonging to the *A. (M.) cameronense* group, is described from the Monts de Cristal in northwestern Gabon. It is actually known from a small number of localities in the Monts de Cristal, which is also the westernmost known distribution area of the *A. cameronense* species group in Gabon. The new species differs from the geographically close populations of other species by the male colouration. The distinct status is also supported by mtDNA data. This is the second endemic nothobranchiid species described from the Monts de Cristal.

Key words. *Aphyosemion cameronense* species group, biodiversity, Central Africa

1. INTRODUCTION

Gabon has, together with Cameroon, the highest diversity of cyprinodontiform fishes in Africa (data from HUBER 2000). The nothobranchiids comprise with almost 50 described species the largest group, many of them with small distribution areas and endemic to Gabon. Several descriptions of new species in recent years demonstrate the limited knowledge of their distribution and diversity (HUBER 1994, 1998a, b, 1999; LEGROS 1999). As large parts of this country are still inadequately known with regard to freshwater fish, the number will certainly grow in the future, and without doubt it is important for biodiversity and conservation considerations to have detailed knowledge on species numbers and distribution.

The Nothobranchiidae are the most abundant and specious group of cyprinodontiform fishes in Gabon (HUBER, 2000). From the Ivindo basin, one of the main Ogoue tributaries in the northern inland, up to eight cyprinodontiform species in syntopy are reported, seven of them nothobranchiids (BROSSET 2003). In the majority of the collection localities a member of the *Aphyosemion (Mesoaphyosemion) cameronense* species group is found. They inhabit a large area in the inland plateau of Cameroon, Equatorial Guinea and Gabon and probably also in the neighbouring areas of the Central African Republic and the Republic of Congo (AMIET 1987; DADANIAK et al. 1995; HUBER 2000). This group actually includes the following described species: *A. (M.) obscurum* (Ahl, 1924a), *A. (M.) amoenum* Radda & Pürzl, 1976, *A. (M.) haasi* Radda & Pürzl, 1976, *A. (M.) halleri* Radda & Pürzl, 1976, *A. (M.) maculatum* Radda & Pürzl, 1977, and *A. (M.) mimbon* Huber, 1977 with mostly small distribution areas in Cameroon and Gabon and the highly polymorphic *A. (M.) cameronense* (Boulenger, 1903) with a large distribution area in the countries mentioned above.

AMIET (1987) was the first who, during his study of the Cameroonian *Aphyosemion* and *Fundulopanchax* species, grouped populations of *A. (M.) cameronense* according to their differing male colour patterns into three 'phenotypes' which he suggested might have full species status. Later, some killifish hobbyists joined their knowledge, accumulated through own field trips, aquarium observations and several publications, about the *A. (M.) cameronense* group in Cameroon and Gabon and classified within *A. (M.) cameronense* six additional 'phenotypes' (DADANIAK et al. 1995). From a taxonomic point of view the status of all these populations, which are often restricted to small areas, still remains unclear. This is mostly due to a lack of clear cut diagnostic male colour patterns and generally an extremly conservative morphology.

The first published evidence of the species described here is given in a report of a collection in Gabon by HUBER (1977, 1980). The author identified this species tentatively as *A.* sp. aff. *obscurum*, because the single collected male shows a superficial similarity with *A. (M.) obscurum* from Cameroon (HUBER 1977, fig. 11). Subsequent collections revealed high variability in male colour patterns as described below (see also figs. on pp.

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[1] In Commemoration of Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004)

29, 416, 421 in DADANIAK et al. 1995 and pp. 66-67 in SEEGERS 1997). Later the species was called *A. cameronense* phenotype 6 by DADANIAK et al. (1995), following the numbering of different phenotypes of the *A. (M.) cameronense* group in Cameroon by AMIET (1987).

Data presented here are mainly based on a collection from Gabon in 2002 where it was possible to find the new species and several other populations of the *A. (M.) cameronense* group, including the formally described species *A. (M.) mimbon* and *A. (M.) maculatum*. Based on material from Gabon and Cameroon collected by the authors and additional material from Equatorial Guinea provided by M. JUHL we also tested the taxonomic status of the new species with mtDNA data.

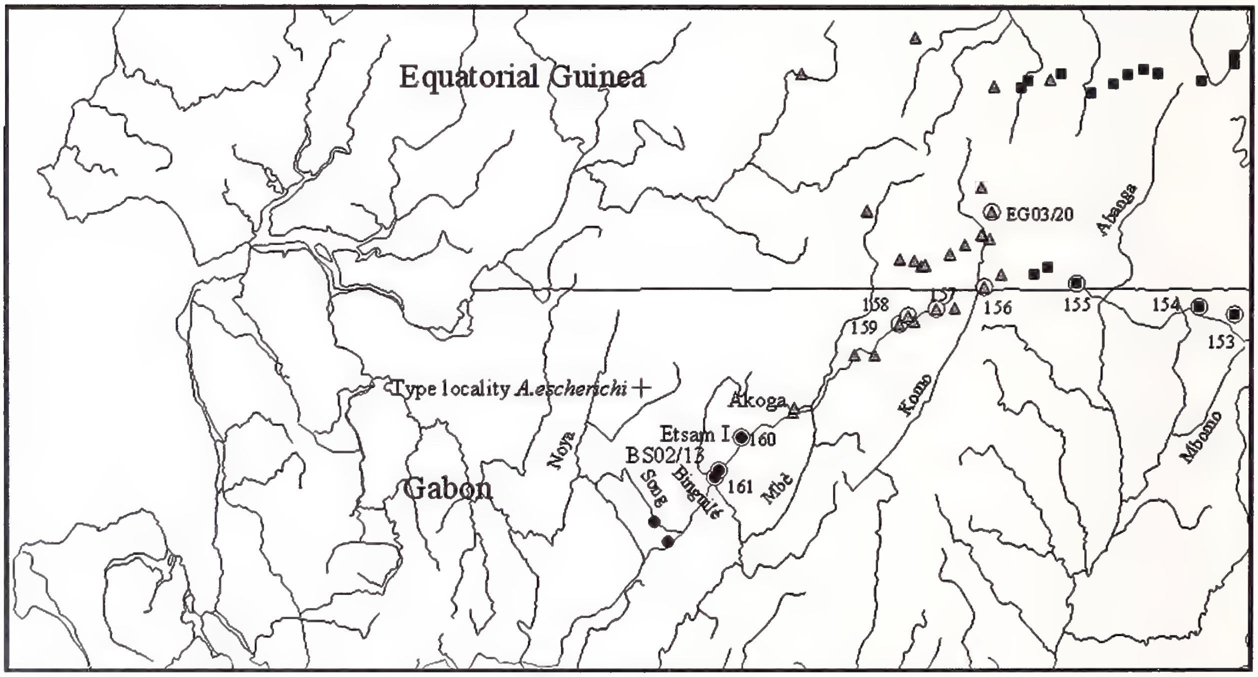
2. MATERIAL AND METHODS

The description is based on specimens collected by the authors during fieldtrips to Gabon 1999 (TB) and 2002 and deposited at the Zoologisches Forschungsinstitut und Museum Koenig, Bonn, Germany (ZFMK). A number of specimens of the type series will be sent to the Musée Royale de l'Afrique Centrale, Tervuren, Belgium (MRAC) and the Institute de Recherche en Ecologie Tropicale (IRET) in Libreville, Gabon.

All fishes were collected with a handnet, sacrified with MS222, preserved in 3,5% Formalin and later transferred to 70% Ethanol for storage. Specimens for DNA studies were stored directly in 96% Ethanol.

Measurements and counts follow AMIET (1987) with the addition of the caudal peduncle, measured from the posterior end of anal fin base to caudal end of peduncle. All measurements are presented as percentages of standard length (SL) and were made point to point with a digital calliper and corrected to the nearest 0.1 mm. Geographical coordinates of sample points visited by the first author are taken with a Garmin GPS 12, map date was WGS 84. The spelling of locality names was taken from the IGN map (Kango, NA-32-V, scale 1:200 000) of this area. The distribution point map is made with the program DIVA-GIS version 4.2 (HIJMANS et al. 2001), GIS files for rivers, roads and country borders are used from the Central African Regional Program for the Environment (CARPE) website (http://carpe.umd.edu/). Additional locality data are provided by M. JUHL, Denmark, U. KÄMPF, Germany (pers. comm. 2003) and from Killi-Data 2000 (HUBER 2000).

Definition and naming of the phenotypes 1-9 follows the definitions of AMIET (1987) and DADANIAK et al. (1995).



Map 1: Known distribution area of *A. (M.) mimbon* ▲, *A. (M.) etsamense* ● and *A. (M.) cameronense* ■ in northwestern Gabon and southern Equatorial Guinea. Type localities of *A. (M.) mimbon* (Akoga), *A. (M.) etsamense* (Etsam I) and *A. escherichi* are shown together with the localities of the DNA samples, which are enclosed in an open circle and numbered according to field locality number (see Table 1). Data from HUBER (2000), own data and M. JUHL, Denmark (pers. comm.).

Table 1: List of specimen used for DNA sequencing with GenBank accession number, voucher number and geographical coordinates of collection localities.

Sampleno.	Species	Collection locality	Country	Genbank accession	Latitude	Longitude
RS 639	*A. (M.) cameronense*	G 02/153	Gabon	AY748279	0°57'38,7"N	11°08'25,3"E
RS 931	*A. (M.) cameronense*	G 02/154	Gabon	AY748280	0°58'18,8"N	11°05'13,2"E
RS 638	*A. (M.) cameronense*	G 02/155	Gabon	AY748281	1°00'22,8"N	10°54'13,0"E
RS 262	*A. (M.) cameronense*	CMM 40	Cameroon	AY748282	2°48'56,1"N	10°40'35,0"E
RS 570	*A. (M.) mimbon*	G 02/158	Gabon	AY748283	0°57'29,7"N	10°39'01,2"E
RS 571	*A. (M.) mimbon*	G 02/159	Gabon	AY748284	0°56'46,0"N	10°38'14,2"E
RS 640	*A. (M.) mimbon*	G 02/157	Gabon	AY748285	0°58'06,3"N	10°41'33,5"E
RS 929	*A. (M.) mimbon*	G 02/156	Gabon	AY748286	1°00'06,0"N	10°45'50,9"E
RS 930	*A. (M.) mimbon*	G 02/159	Gabon	AY748287	0°56'46,0"N	10°38'14,2"E
RS 974	*A. (M.) mimbon*	EG 03/20	Equatorial Guinea	AY748288	1°06'47,2"N	10°46'31,1"E
RS 545	*A. (M.) etsamense*	G 02/160	Gabon	AY748289	0°46'34,1"N	10°24'03,0"E
RS 577	*A. (M.) etsamense*	BS 02/12	Gabon	AY748290	0°46'34,1"N	10°24'03,0"E
RS 604	*A. (M.) etsamense*	G 02/160	Gabon	AY748291	0°46'34,1"N	10°24'03,0"E
RS 633	*A. (M.) etsamense*	G 02/160	Gabon	AY748292	0°46'34,1"N	10°24'03,0"E
RS 923	*A. (M.) etsamense*	G 02/160	Gabon	AY748293	0°46'34,1"N	10°24'03,0"E
RS 924	*A. (M.) etsamense*	G 02/160	Gabon	AY748294	0°46'34,1"N	10°24'03,0"E
RS 925	*A. (M.) etsamense*	BS 02/13	Gabon	AY748295	0°43'36,9"N	10°21'58,1"E
RS 1355	*A. (M.) etsamense*	G 02/161	Gabon	AY748296	0°42'58,1"N	10°21'37,0"E

The specimens used in the DNA analysis are listed in Table 1 and were deposited in the tissue collection of the ZFMK. Map 1 shows the localities of the DNA samples. We sequenced a part of the mitochondrial cytochrome b gene, a detailed description of the method will be given in a subsequent paper.

The resulting sequences were aligned by eye in BioEdit 5.0.9 (HALL 1999) and uncorrected pair-wise sequence divergence calculated with MEGA 2.1 (KUMAR et al. 2001). The sequences were deposited in GenBank, accession numbers are listed in Table 1. Here we used the molecular data set only to get additional information on the distinctness of the species described here from its closest relatives and not to reconstruct a phylogeny of this complex species group.

As indicators for species status we use distinctness of colour pattern with respect to all surrounding populations of other related species and in addition the monophyletic cluster of mitochondrial haplotypes. This is seen as indirect evidence for different biospecies sensu MAYR.

3. RESULTS

***Aphyosemion (Mesoaphyosemion) etsamense*, new species** (Figs. 1-4)

Aphyosemion sp. aff. *obscurum* Huber, 1977:6 (in part, only locality 55), fig. 11, 1980:38 1996:333, 2000:480

Aphyosemion sp. aff. *cameronense* Phänotyp 6, Dadaniak et al., 1995:416-424 , figs. pp. 29, 416, 421

Aphyosemion sp. aff. *cameronense* [Pop. 6], Seegers, 1997:66-67, 3 figs.

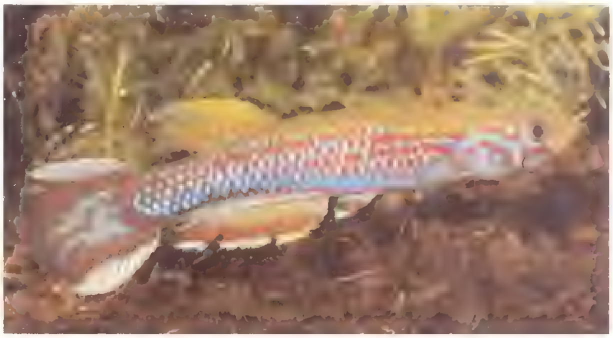


Fig. 1: *Aphyosemion (Mesoaphyosemion) etsamense* sp. nov., male, same locality as Type, not preserved.

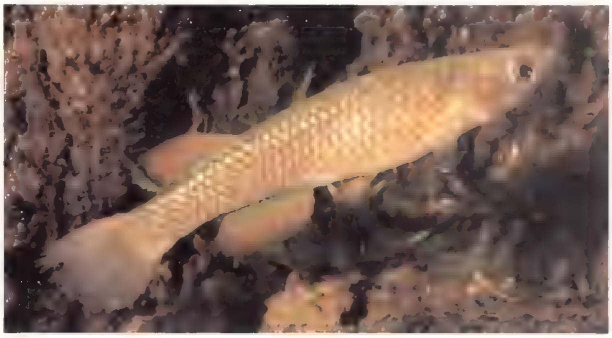


Fig. 2: *Aphyosemion (Mesoaphyosemion) etsamense* sp. nov., female, same locality as Type, not preserved.

Holotype: ZFMK 39832, male, 32,4 mm SL; Gabon, western slopes of the Monts de Cristal, a small river at the village Etsam I, crossing the road N5 from Medoneu to Kougouleu (0°46'34,1" N, 10°24'03" E), collected 29. July 2002 by T. Blum, G. Fleck and R. Sonnenberg, collection locality G 02/160.

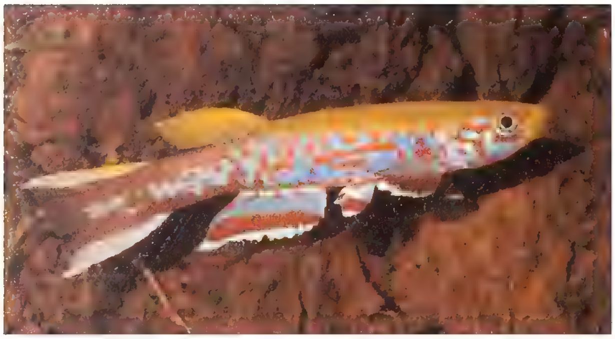


Fig. 3: *Aphyosemion (Mesoaphyosemion) etsamense* sp. nov., male from a locality north of Assok (BS 02/13), not preserved

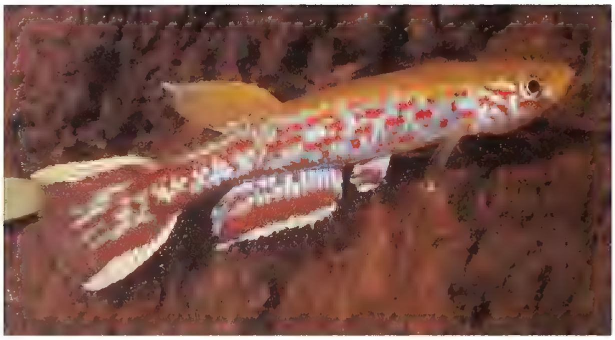


Fig. 4: *Aphyosemion (Mesoaphyosemion) etsamense* sp. nov., male from Assok, not preserved

Paratypes: MRAC A4-42-P-1-4, same data as holotype, ZFMK 39833 – 39842, same data as holotype, ZFMK 39843, male, Gabon, north of the village Assok, collected 11. September 2002 by T. Blum and P. Sewer, collection locality BS 02/13 (0°43'36,9" N, 10°21'58,1" E). ZFMK 39844 - 39846, collected by F. Bitter, T. Blum and P. Sewer in August 1999, same locality data as holotype, preserved after approximately 2 years in aquarium. IRET, Gabon, two specimens, one male and one female, same data as holotype.

Additional Material: Colour pictures of live specimens of the above and other populations of the *A. cameronense* group are used to compare colour patterns (Amiet 1987; Dadaniak et al. 1995; Huber 1977; Seegers 1997).

Diagnosis: *Aphyosemion* (*Mesoaphyosemion*) *etsamense* is distinguished from other species of *Aphyosemion* by its unique combination of colouration characters in males. This distinctness is supported by a monophyletic lineage of mtDNA haplotypes.

Males of *A. (M.) etsamense* are distinguished from all other members of this species group by its nearly complete yellow dorsal fin with small irregular red dots only on basal and posterior egde of fin versus blue or pale yellow with more red dots or flames (compare *A. (M.) cameronense* Figs. 10-12). The only exceptions are *A. (M.) mimbon* (Figs. 5 and 6) and a population of *A. (M.)* cf. *cameronense* in the Ivindo basin between Makokou and Ovan (Fig. 16), which are distinguished by their different body, caudal, and anal fin colouration. *A. (M.) etsamense* is also distinguished from all species and phenotypes with a yellow caudal peduncle (*A. (M.) amoenum* (Fig. 8), *A.(M.) halleri*, *A.(M.)* sp. aff. *cameronense* phenotype 3, 4, 5 (Fig. 14) and 9) through its complete blue colouration of the sides in males versus blue or bluegreen with a yellow or orange peduncle. It is distinguished from *A. (M.) maculatum* (Fig. 9), *A. (M.) mimbon* (Figs. 5 and 6) and *A.(M.)* sp. aff. *maculatum* from Equatorial Guinea by the pattern of the red pigmentation on the males side. In *A. (M.) etsamense* the pigmentation is arranged in horizontal rows of dots which can fuse to closed or irregularly interrupted lines and in some specimens with red reticulation on the caudal peduncle versus more vertical distribution of red pigment clusters and horizontal rows of red dots only on anterior part of body and less extensive reticulated pattern (see Figs. 1, 3, 4, 5, 6, 10 for comparison). It differs from *A. (M.) obscurum* (Fig. 7) and *A. (M.)* sp. aff. *cameronense* phenotype 1 (Fig. 13) and 4 by the variability of the red colour pattern, which exceeds the observed variation in both species and the yellow dorsal and the sometimes yellow marginal bands in the caudal and anal fins in most specimens versus always white bands in the other three.

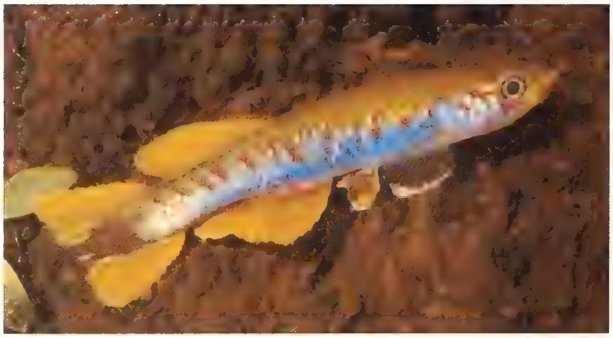


Fig. 5: *Aphyosemion (Mesoaphyosemion) mimbon* from locality BBS 99/23, same as G 02/157

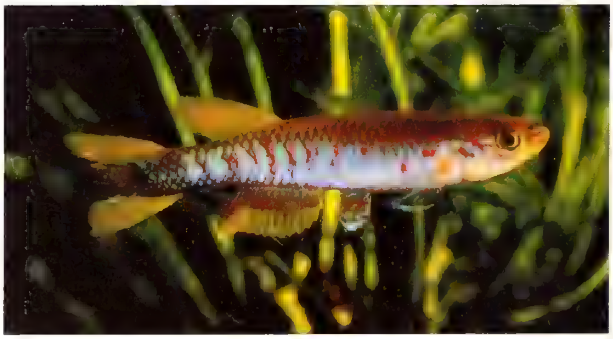


Fig. 6: *Aphyosemion (Mesoaphyosemion) mimbon* from locality GEB 94/25, same as G 02/158

It differs from *A. (M.)* sp. aff. *cameronense* phenotype 8 (Fig. 15) by a different colour pattern on the fins and more red markings on the sides, where phenotype 8 has less markings and more red dots in the dorsal and finer red markings in the caudal fin.

Description: See Figs. 1 – 4 for general appearance and Table 2 for morphometric data of the type series. A slender and elongate medium sized *Mesoaphyosemion* species. Snout is rounded, mouth directed upwards, posterior end of mouth at same level as center of the eye. Dorsal profile straight. Shows, like most cyprinodontiform fishes, a strong sexual dimorphism. Adult males more colourful and larger than females. Dorsal and anal fin in males slightly pointed, caudal fin trapezoid with slightly rounded posterior end, no filamentous extensions like in the *A. calliurum* group for example. Fins in females in general smaller and rounded. Dorsal fin origin behind origin of anal fin (D/A = +7 – +8) and behind mid length of body. Dorsal fin with 11 – 13 rays, anal fin with 15 – 16 rays, scales on mid-longitudinal series 31 – 33 + 2 – 3 on caudal fin base. Transverse rows of scales above pelvic fin 8 – 10, circumpeduncular scale row 13 - 14.

Table 2: Morphometrics of *Aphyosemion etsamense*. All measurements in percents of standard length (SL), except standard length in mm. TL= total length, PD= predorsal fin distance, HL= length of head, pPD= prepelvic fin distance, pAD= preanal fin distance, HB= greatest body height, HC= height of caudal peduncle, CL= length of caudal peduncle, BD= base of dorsal fin, BA= base of anal fin, D= dorsal fin rays, A= anal fin rays, D/A= dorsal / anal fin position, E= eye diameter, I= interorbital width, LLS= lateral line scales, TS= transverse row of scales, CS= scales around caudal peduncle, SD= standard deviation.

	TL	SL	PD	HL	pPD	pAD	HB	HC	CL	BD	BA	D	A	D/A	E	I	LLS	TS	CS	CL/HC
Holotype	125,4	32,4	65,4	28,1	43,7	58,5	20,3	12,1	23,6	14,4	19,5	12,0	16,0	8,0	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Paratypes mean (♀)	124,7	30,4	67,9	26,2	45,8	60,5	18,4	10,4	22,5	13,7	20,1	12,3	15,5	8,0	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Paratypes mean (♂)	125,7	29,2	68,6	27,3	47,1	59,6	18,8	10,9	22,2	14,5	21,2	12,3	15,6	7,8	[illegible]	11,6	[illegible]	[illegible]	[illegible]	[illegible]
all types mean	125,3	29,8	68,2	26,9	46,4	59,9	18,7	10,8	22,4	14,2	20,7	12,3	15,6	7,9	[illegible]	11,8	[illegible]	[illegible]	[illegible]	[illegible]
all types SD	2,6	5,4	2,6	1,4	3,0	2,2	1,1	0,6	1,1	0,9	1,3	0,6	0,5	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

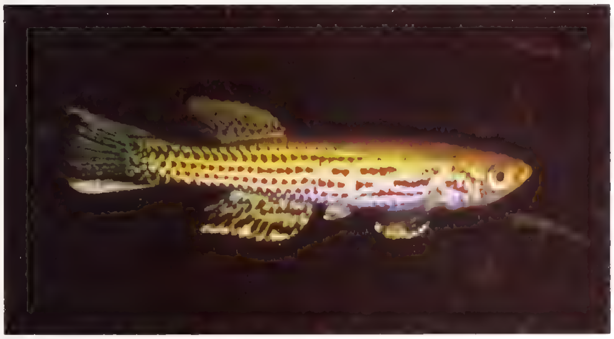


Fig. 7: *Aphyosemion (Mesoaphyosemion) obscurum*, near Matomb, Cameroon.

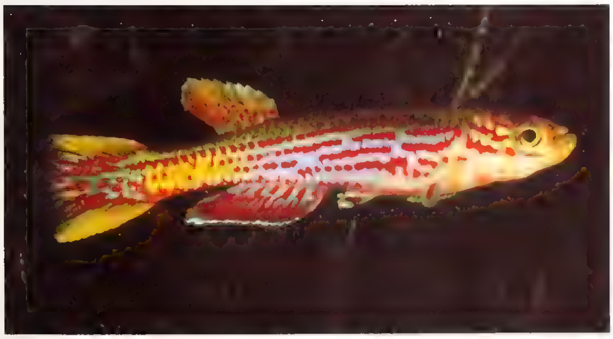


Fig. 8: *Aphyosemion (Mesoaphyosemion) amoenum*, Cameroon.

Coloration: Living males (Figs. 1, 3, 4): snout yellow, dorsal part of body from mouth to dorsal fin base brown to yellow, beneath eye a red sub-ocular line, on operculum three oblique bands of fused red dots, the upper in some specimens overlayed by yellow colouration of the back; sides light blue, with brilliant hue, but not as metallic as in other species; on sides posterior to operculum rows of red dots, forming up to four more or less continuous rows; in some specimen additional short rows, one starting below dorsal fin to caudal and one ventral behind pectoral fin which can fuse with ventral red band which is seen in most *A. (M.) cameronense* group fishes. The red colouration can also be irregularly interupted or fuse to red bands or blotches on caudal body sides, where it often forms a reticulated pattern on the caudal peduncle.

Dorsal fin mainly yellow, with blue only on basal and posterior part, with red dots or flames basal and posterior distal. Anal fin colour ranging from light blue to almost completely yellow with small basal blue part, several specimens with red dots or flames on basal part; submarginal red band of varying size, marginal band white, blueish or yellow, in some specimens white with partially yellow. Caudal fin colour pattern also variable; center light blue with horizontal red flames or dots; red on anterior, posterior and submarginal parts often fused which encloses the blue central part; upper and lower marginal band white, bluish grey or yellow, as in anal fin often yellow and white combined. Pectoral fins transparent with marginal blue, pelvic fins blue, with submarginal red band and white or blue marginal similar to anal.

Living females (Fig. 2): body brown, dorsally darker than ventrally; red dot at end of scales, fusing to a reticulated pattern on caudal peduncle, traces of red subocular line and three oblique red lines on operculum

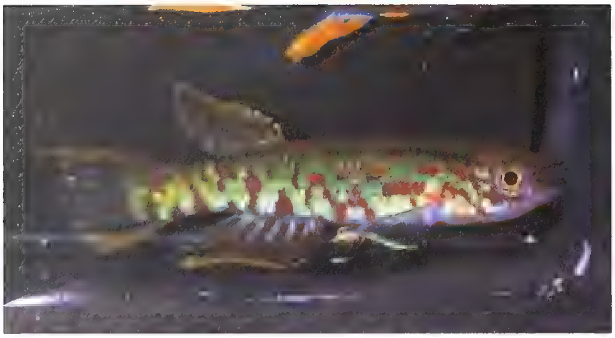


Fig. 9: *Aphyosemion (Mesoaphyosemion) maculatum*, near Matora, collection loc. G 02/125, Gabon

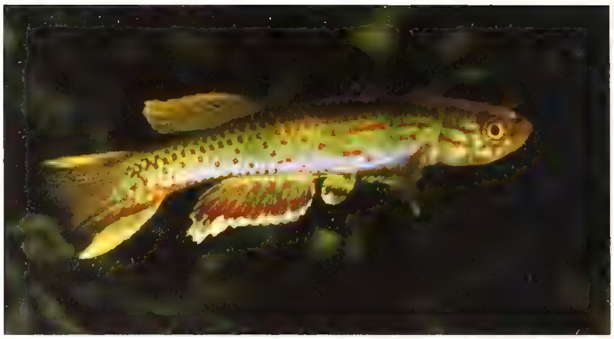


Fig. 13: *Aphyosemion (Mesoaphyosemion)* sp. aff. *cameronense* phenotype 1, near Mvilé, Cameroon

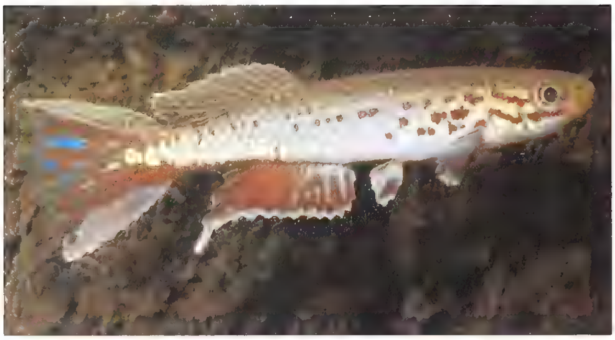


Fig. 10: *Aphyosemion (Mesoaphyosemion) cameronense*, collected in Gabon at Olong II near the border to Equatorial Guinea, G 02/149

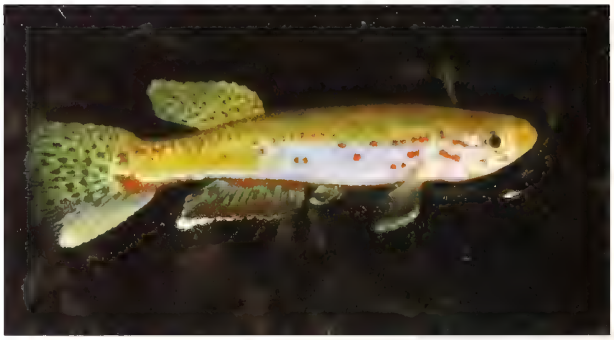


Fig. 14: *Aphyosemion (Mesoaphyosemion)* sp. aff. *cameronense* phenotype 5, near Koumaméyong, Gabon

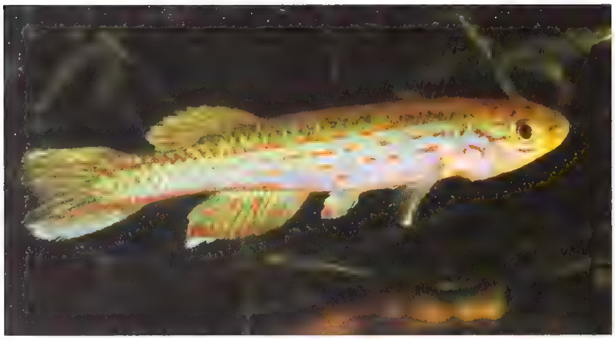


Fig. 11: *Aphyosemion (Mesoaphyosemion) cameronense* from Cameroon, between Akom II and Ebolowa, collecting loc. CMM 40

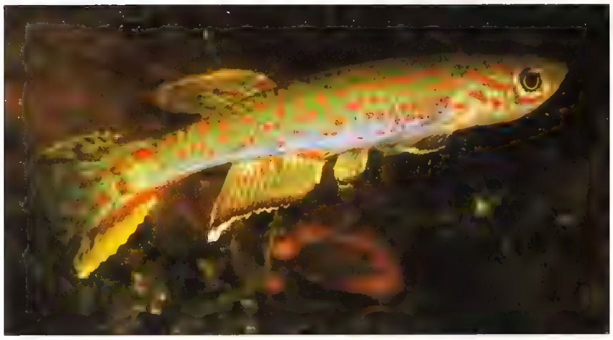


Fig. 15: *Aphyosemion (Mesoaphyosemion)* sp. aff. *cameronense* phenotype 8, West Mitzic, Gabon

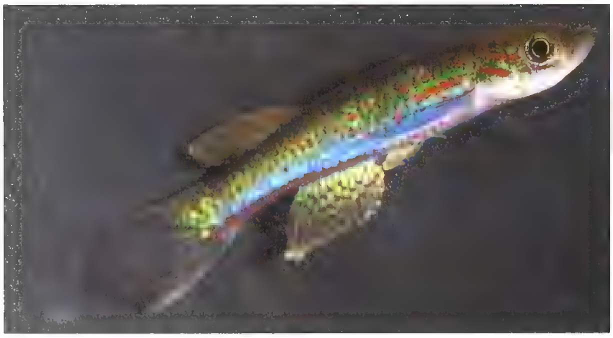


Fig. 12: *Aphyosemion (Mesoaphyosemion) cameronense* from the IRET Research Center near Makokou, G 02/126

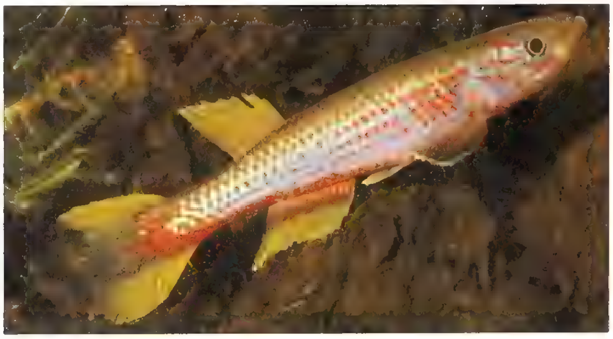


Fig. 16: *Aphyosemion (Mesoaphyosemion)* cf. *cameronense* BSW 99/11, between Makokou and Ovan at Minkwala.

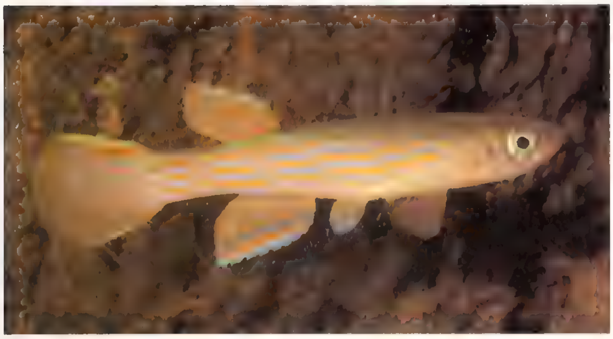


Fig. 17: *A. escherichi*, aquarium raised male from northern Gabon

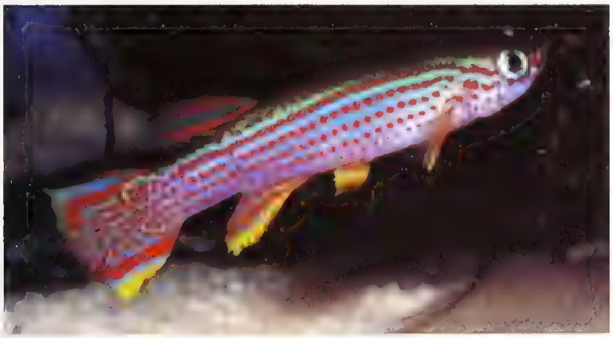


Fig. 18: *A. striatum*, aquarium raised male from Cap Esterias, Gabon

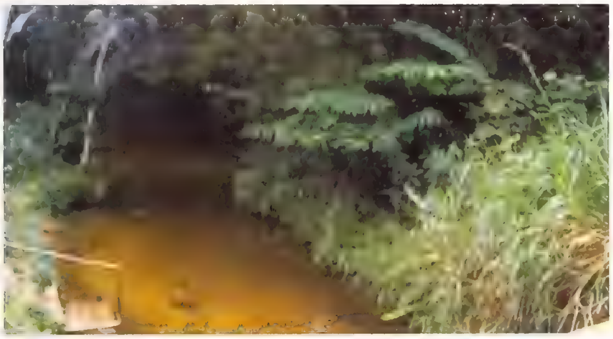


Fig. 19: Type locality of *Aphyosemion (Mesoaphyosemion) etsamense* at Etsam I, Gabon

All unpaired fins and pelvic fins transparent with interradial red flames; anal and pelvic fins with traces of a small blueish marginal band, pectoral fins transparent with small whitish marginal band.

Preserved in Ethanol: Males: body brown, upper part darker than lower, belly light brown, dark pigment on scales forming a reticulated pattern posterior to operculum; fins pale grey, dorsal distal and posterior part with dark brown interradial flames, on caudal and anal fin whitish marginal bands, submarginal dark brown bands, posterior end of caudal dark brown, interradial dark brown flames; pelvic and pectoral fins pale grey, with submarginal dark brown and small whitish marginal band.

Females: body brown, upper and dorsal part dark brown, belly light brown, dark pigment on scales forming a reticulated pattern posterior to operculum; all fins pale grey with dark brown interradial flames on all except pectorals.

DNA data: The alignment contains 800bp for a set of 18 specimens in total, 8 *A. (M.) etsamense* from 3 different localities, 6 *A. (M.) mimbon* from 5 localities and 4 *A. (M.) cameronense* from 4 localities.

115 positions are variable, 89 might be phylogenetically informative. There are ten unambiguous potential synapomorphic positions in the sequences of *A. (M.) etsamense*. 14 positions are ambiguous in having whithin one *A. (M.) etsamense* (specimen RS 925) a character state also found in the outgroup (9) or one outgroup specimen having a state like in *A. (M.) etsamense* (5).

The amount of uncorrected pair-wise sequence divergence between *A. (M.) etsamense* and *A. (M.) mimbon* is 4,25 - 6,63 % and between *A. (M.) etsamense* and the other specimens tentatively identified as *A. (M.) cameronense* 6,25 - 8,37 %. The divergence between *A. (M.) mimbon* and *A. (M.) cameronense* is 5,62 - 6,88 %. Within *A. (M.) etsamense* sequence divergence is up to 2,25 % and, in comparison, within *A. (M.) mimbon* up to 3,13 %. We want to state that we use the distinctiveness of haplotypes with their potential apomorphic character states and not the genetic distance value as additional indicator for species status together with the colouration characters which unite the groups of populations from the different species.

Etymology: This species is named after the village Etsam I, Gabon, at the type locality (Fig. 19).

Distribution and habitat: Only known from some populations found in rivulets along the road N5 between Medouneu and Kougouleu: localities near the villages Etsam I, Assok and Song (Map 1). The closest known locality of *A. (M.) mimbon* is the village Ntom (DADANIAK et al. 1995), ca. 2 km south of Akoga, which is the type locality of this species (HUBER 1977) and approximately 15 km north of Etsam I. According to the official map (Kango, NA-32-V, scale 1:200 000) all localities of *A. (M.) mimbon* in Gabon are found in tributaries of the Komo and the Mbè, those of *A. (M.) etsamense* except at Song seem to belong to the Binguilé which is also a tributary of the Mbè below the Barrage de Tchimbélé. The rivulets around the village Song empty into the Song river, a tributary of the Noya. The closest localities east of Medouneu are populated by fishes identified as *A. (M.) cameronense* s.s. (DADANIAK et al. 1995) and are found in tributaries of the Mvo and Abanga rivers.

Habitats are small rainforest creeks and rivers with slow flowing water. The type locality (Fig.19) is a larger, slow flowing river, about 3-4 m wide and up to 0,8 m deep. This is a rather unusual habitat for species of the *A. (M.) cameronense* group which are usually found in rivulets not that deep. The fishes are all found between the terrestrial vegetation which hangs into the water, in addition they are also found in smaller rivulets emptying into the main river. The other known localities are small rainforest creeks between 0,5 and 2,0 m wide and usually not deeper than 0,4-0,5 m.

Remarks: Because *A. (M.) etsamense* could be found near Song (HUBER 1977, locality JH 55) within rivulets emptying into the Song river, which itself is a tributary to the Noya river (Nduya river according to WILDEKAMP 1993 and SEEGERS 1987, 1988, Nga river according to AHL 1924b) it is necessary to discriminate between *A. (M.) etsamense* and *A. escherichi* (AHL 1924b) as the type locality of the latter is at 'Attogondema, Nga-Zuflüsse, Kamerun' (AHL 1924b).

In this area the two species *A. escherichi* and *A. striatum* (Boulenger, 1911) are often found in syntopy and both species have a very similar colour pattern (Figs 13 and 14).

Whereas SEEGERS (1988) and WILDEKAMP (1993) list *A. escherichi* as a valid species with the junior synonyms *A. microphtalmum* Lambert & Gery, 1967 and *A. simulans* Radda & Huber, 1976, HUBER (1998c, 2000) is of the opinion that it represents a junior synonym of *A. striatum* (Boulenger, 1911). As *A. (M.) etsamense* occurs in the same river system like the former two species, we have to show that the new species is not conspecific with *A. escherichi*.

HUBER (1998c) based his opinion on small morphological differences, mainly dorsal and anal fin ray and vertebrae counts, although the species have a nearly complete overlap in these morphological values (Table 3). The vertebrae counts given by HUBER (1998c) for *A. striatum* and *A. microphtalmum* (mean 27,50 and 27,70 respectively) are closer to each other than to the type series of *A. escherichi* (mean 29,55), so if they had a discriminatory value, then *A. striatum* and *A. microphtalmum* were closer together than to *A. escherichi* and the latter might represent a distinct species. Because of the large overlap, the previously listed morphological features have no discriminatory value in this case, and for a statistical significant distinction the number of specimens and samples had to be considerably larger.

Table 3: Comparison of morphometric data from *A. escherichi, A. microphtalmum, A. striatum* (from HUBER, 1998c) and *A. (M.) etsamense*

	A. striatum (n = 8)	*A. microphtalmum* (n = 3)	*A. escherichi* (n = 11)	*A. (M.) etsamense* (n = 21)
Dorsal fin rays	10-11	10-11	11-12	11-13
Mean	10.75	10.33	11.18	12.29
Anal fin rays	14-16	16-17	13-15	15-16
Mean	14.88	16.33	13.91	15.57
D/A deviation	+5 - +7	+7 - +8	+5 - +6	+7 - +8
Mean	6.00	7.67	5.82	7.90

On the other hand, according to SEEGERS (1988) and WILDEKAMP (1993) and own observations, the major differences between *A. striatum* versus *A. escherichi* and *A. (M.) etsamense* are the obviously different colour patterns of the fins, especially the dorsal fin (Fig. 1, 3, 4, 17, 18). This character seems to be stable throughout the distribution area of the species. In addition the different relation between caudal peduncle length and height is a diagnostic character. These characters are also mentioned in the first descriptions by AHL (1924b) and HOLLY (1930), who restudied AHL'S type series, for *A. escherichi* (caudal peduncle nearly 2 x height in length) and by BOULENGER (1911) for *A. striatum* (caudal peduncle about 1,33 x height in length).

Despite the absence of significant differences in the caudal peduncle between *A. escherichi* and *A. (M.) etsamense* (2,0 - 2,2 x times height in length, Table 2), the male colouration allows the identification of both species (see Figs. 1, 3, 4, 17) and also the discrimination between *A. (M.) etsamense* and *A. striatum* (Figs. 1, 3, 4, 18). The dorsal fin in *A. (M.) etsamense* shows little blue or red pigmentation on the posterior or basal part versus little yellow with lots of red pigmentation in *A. escherichi* (dots and flames). *A. striatum* shows two parallel horizontal bands on blue or yellow background, the caudal peduncle height about 1,33 times in length. The often very regular horizontal rows of red dots on body sides in males in *A. escherichi* and *A. striatum* are clearly an unrealiable discriminatory character to the irregular red pigmentation in *A. (M.) etsamense*, because on one hand we found several *A. (M.) etsamense* males which also show a more or less regular pattern of horizontal red dots, on the other hand we found especially in the area of the Monts de Cristal populations of *A. striatum* with a very irregular pigmentation similar to the former species.

4. DISCUSSION

In general it is difficult to find diagnostic characters to discriminate other species against the heterogenous assemblage of populations which is summed up in the taxon *A. (M.) cameronense*. However, the discrimination between *A. (M.) etsamense* and its genetically and geographically closest relative, *A. (M.) mimbon* is easy due to the different colour patterns (see Figs. 5, 6). Also the distinction to the geographically close populations we collected between Sam and Medouneu in the tributaries of the Mvo and Abanga rivers and most other populations, which are identified as *A. cameronense* (Figs 10-12) (DADANIAK et al. 1995; HUBER 2000), is possible because of their differing phenotype with little red pigmentation on the sides of males.

Mesoaphyosemion: The taxon *Mesoaphyosemion* was erected by RADDA (1977) as a subgenus of *Aphyosemion*. As type species he chose *A. cameronense* (BOULENGER, 1903). However, RADDA also included in his newly erected subgenus all those species groups which show a superficial similarity in morphology and therefore turned this group into a taxonomic 'wastebasket'. Actual research by MURPHY & COLLIER (1999) based on DNA sequences confirm that *Mesoaphyosemion* is not a monophyletic group. In this paper we suggest to restrict the taxon name *Mesoaphyosemion* Radda, 1977 to the *A. (M.) cameronense* species group and exclude all other species which then makes *Mesoaphyosemion* a monophyletic or natural group. This group now contains the following described species: *A. (M.) cameronense* (Boulenger, 1903), *A. (M.) obscurum* (Ahl, 1924a), *A.(M.) amoenum* Radda & Pürzl, 1976, *A. (M.) haasi*, Radda & Pürzl, 1976, *A. (M.) halleri* Radda & Pürzl, 1976, *A. (M.) maculatum* Radda & Pürzl, 1977, *A. (M.) mimbon* Huber, 1977 and *A. (M.) etsamense*. It includes also the undescribed, but recognizable groups of populations defined by AMIET (1987) and DADANIAK et al. (1995) with their different male colour patterns, which might, like *A. (M.) etsamense*, be regarded as distinct species.

This is the second described endemic species of nothobranchiid fishes in the Monts de Cristal besides *A. (M.) mimbon*. For the nothobranchiids it is a species poor area, as only one other species group of *Aphyosemion* and very rarely a species of *Episemion* could be found in syntopy with a *Mesoaphyosemion* species (HUBER 1977, 2000; own data). For comparison, whithin the Ivindo basin the highest number is seven species of different species groups (Brosset 2003) and for the coastal plain up to five or six species of different groups in syntopy (own observations). Further collections might reveal a higher diversity, as only a small part of this area is known with regard to cyprinodontiform fishes.

Résumé. *Aphosemion (Mesoaphosemion) etsamense* sp nov., une espèce du groupe *A. (M.) cameronense*, est décrite des Monts de Cristal du nord-est du Gabon. Cette espèce n'est connue que d'un petit nombre de localités situées dans les Monts de Cristal ce qui en fait l'espèce du groupe cameronense à la distribution la plus occidentale. Cette espèce nouvelle se différencie des populations des autres espèces géographiquement proche par la coloration du mâle. Son statut d'espèce à part entière est également supporté par l'analyse d'ADN mitochondrial. Elle représente la deuxième espèce endémique de nothobranchiid des Monts de Cristal.

Acknowledgements. The authors thank the Ministry of Scientific and Technical Research (MINREST), Yaounde, Cameroon, the Institut de Recherche Agricole pour le Développement (IRAD), Yaounde, the IRAD Fisheries & Oceanography Research Station, Batoke, Limbe, Cameroon, for research permisson and support in Cameroon, the Centre National de la Recherche Scientifique et Technologique (CENAREST) and the Institut de Recherche en Ecologie Tropicale (IRET), especially Prof. Dr. P. Posso, for research permisson and support in Gabon . We would also like to thank Dr. G. Fleck, Bonn for his support during the time in Gabon and the translation of the french abstract, F. Herder, PD Dr. B. Y. Misof, A. C. Schunke for their comments on earlier drafts of the manuscript and U. Kämpf for providing excellent slides for publication. We also want to thank C. Akum and family and C. E. Gabche and family, Limbe, Cameroon for their generous help and support, and Dr. A. Kamdem Toham, WWF, Libreville, Gabon for his help. We like to thank F. Bitter, W. Eigelshofen, Dr. J. H. Huber, M. Juhl, the Kämpf family, Dr. H. Kullmann, K.-H. Lüke, Dr. L. Seegers, A. Tränkner, R.H. Wildekamp, all colleagues at the molecular lab of the ZFMK and a lot of other people too much to be listed here for various support.

Both authors would like to thank especially all those friendly people in Cameroon and Gabon who helped us during fieldwork.

A part of this work was financed by the DFG Project MI-649/2-1, a travel grant for Cameroon was provided to RS by the Alexander-Koenig-Stiftung, Bonn.

Rainer Sonnenberg wishes to dedicate this paper to the late Professor Dr. C. M. Naumann, in memory of his continuous support and encouragment during all my years at the ZFMK in Bonn. His comments, critics and help will be missed.

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Bonner zoologische Beiträge | Band 53 (2004) | Heft 1/2 | Seiten 221–225 | Bonn, Juni 2005

Ambia naumanni sp. n., a New Species of Musotiminae from Yunnan (Lepidoptera, Crambidae)[1]

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Abstract. *Ambia naumanni* sp. n. is described from Lijiang (Yunnan, China) and differentiated from related species. The following new combinations are proposed: *Ambia colonalis* (Bremer, 1864) **comb. n.** (described as *Hydrocampa*) and *Ambia locuples* (Butler, 1889) **comb. n.** (described as *Oligostigma*).

1. INTRODUCTION

In the revision of the Palearctic Acentropinae (SPEIDEL 1984), all the species of the Palearctic part of China recognized to belong to this subfamily have been revised. However, one Chinese species – which was found to be undescribed – turned out to be misplaced in the Acentropinae and remained without an identification and name, as it was excluded from the study. It was recognized to belong to another subfamily: Musotiminae.

The Musotiminae were formerly included in the Nymphulinae (= Acentropinae) (e.g. HAMPSON 1897; MUNROE 1972), but separated as an independant subfamily by SPEIDEL (1981), a treatment which is now generally accepted (MUNROE & SOLIS 1999; SOLIS & MAES 2002).

The authors found additional specimens of this musotimine species in the collection of the Alexander Koenig Research Institute and Museum of Zoology (ZFMK) and decided to describe the species as new, a plan which remained unrealised for a long time, because of the problem of the association with a reasonable genus. There is no revision of the subfamily in a world-wide scale, and there are several genera recognised in the subfamily, and a few more can still be found misplaced among other subfamilies. It finally became clear that the species belongs either to *Musotima* Meyrick, 1884 or to *Ambia* Walker, 1859. To our opinion, the present species fits quite well in the latter genus. However, several obviously closely related species from Japan were treated in the genus *Musotima* (YOSHIYASU 1985) and so there remained some uncertainty about its generic position.

Later we found that the figures of the genitalia of the generic type-species *Ambia ptolycusalis* Walker, 1859 by LANGE (1956) are incorrect. They represent a misidentified acentropine species, a member of the genus *Paracymoriza* of the group of *P. eromenalis* (Snellen, 1880) and *parallelalis* Sauber, 1902. Therefore, we here provide a correct figure of the holotype of *Ambia ptolycusalis* and its genitalia from Sarawak, Borneo (Hope Entomological Collections, University Museum, Oxford) (Figs 8, 9). Both figures clearly show that *A. ptolycusalis* represents another species and belongs to an entirely different subfamily. The wrong figure given by LANGE is probably the reason why YOSHIYASU (1985) did not use *Ambia* for any species treated in his revision. To our opinion, *Musotima* has to be synonymized with *Ambia* or at least a part of the species treated under *Musotima* by YOSHIYASU have to be transferred to *Ambia*. We do not propose a formal synonymisation of *Ambia* and *Musotima* here, as the systematics of the subfamily is presently in a process of development and changes: Very recently, two new genera are named and others are new defined in order to establish monophyletic entities (SOLIS et al. 2004; YEN et al. 2004) which will eventually make it necessary to split the genus *Ambia* as well.

Ambia ptolycusalis has a typical spine-like saccular process (see fig. 9) which does not occur in any species of the subfamily Acentropinae and which is not present in LANGE's misidentified figure. It is also found in *Ambia colonalis* (Bremer, 1864) **comb. n.** (described as *Hydrocampa*) and specimens which we associate with the description of *Ambia locuples* (Butler, 1889) **comb. n.** (described as *Oligostigma*). This spined sacculus is also found in other crambid subfamilies, e.g. in the Scopariinae. Therefore, it seems difficult to use this character as an autapomorphy of *Ambia*, especially as apparently closely related species lack this process.

In the present new species, the saccular spine is absent, but there is a conspicous, angled process to the aedeagus, arising dorsally close to the insertion of the ductus ejaculatorius. We also found this apomorphic character in a species identified as *Ambia locuples* which is, on the other hand, provided with a saccular spine. The furcated aedeagus is a rather rare character in *Ambia* and absent in other Musotiminae, but it is weakly indicated also in the type-species *A. ptolycusalis*. However, generic separation of species with such an unusual

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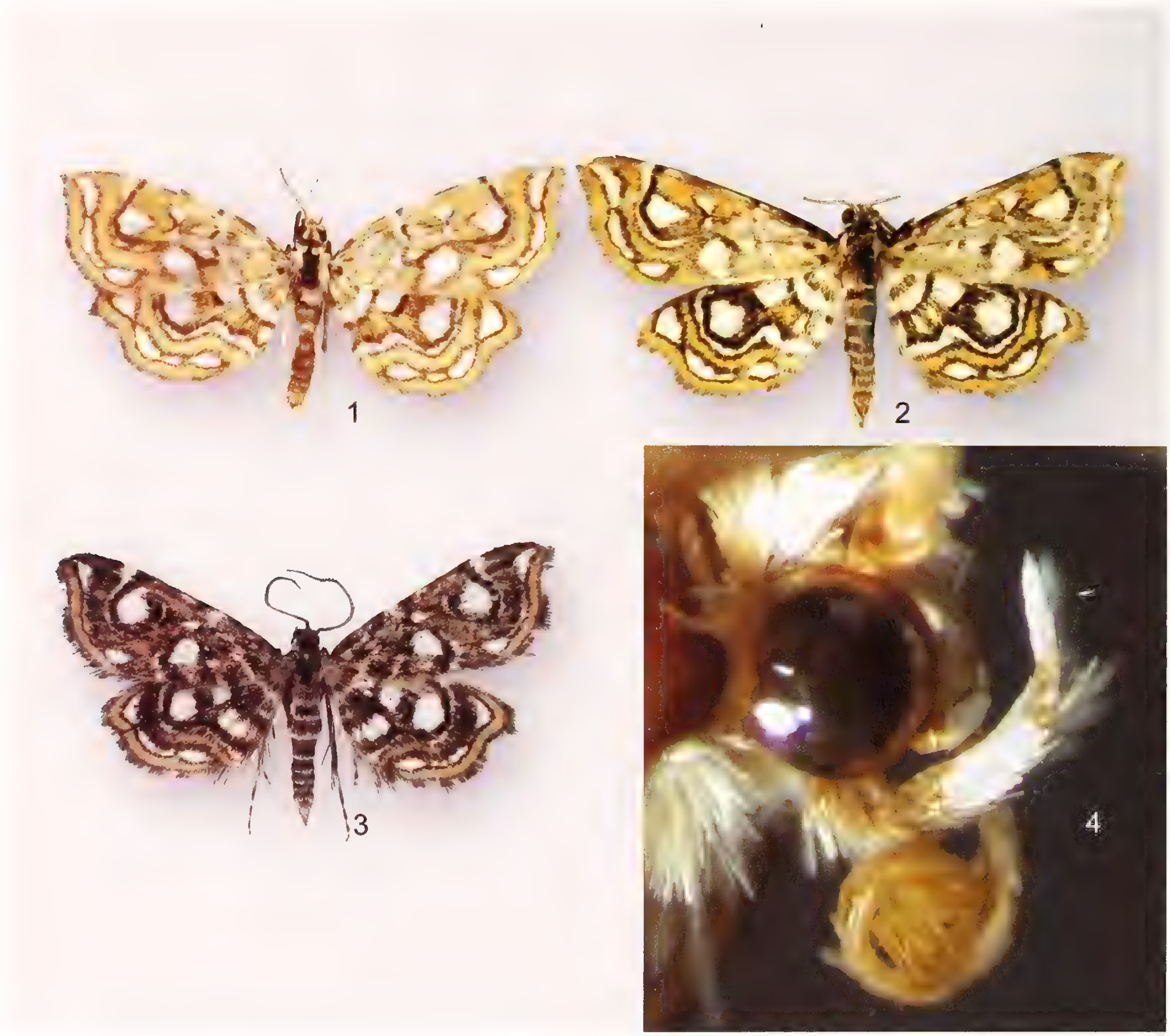
[1] In commemoration of Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004)



Figs. 1–4:
1. *Ambia naumanni* sp. nov., holotype, male (Lijiang, 8. viii. 1934) (wing span 15 mm).
2. *Ambia naumanni* sp. nov., paratype, male (Lijiang, 13. vi. 1934) (wing span 16 mm).
3. *Ambia thyridialis* (Lederer, 1855), male (Ghazir) (wing span 15 mm).
4. *Ambia naumanni* sp. nov., male paratype, lateral view of head.

aedeagus-structure as found in *Ambia locuples* and the new species seems not advisable. We consider *Ambia thyridialis* (Lederer, 1855) (fig. 3), a species recorded from the Lebanon and Egypt which also has no saccular tooth as a closely related species.

2. DESCRIPTION OF SPECIES

Ambia naumanni **Speidel & Stüning, sp. nov.** (Fig. 1, 2)

Holotype ♂: "Li-kiang. (China). Provinz Nord-Yuennan. 8. 8. 1934. H. Höne"

Paratypes: Males: dto. 1 ♂ 13. 6. 1934; 1 ♂ 19. 7. 1934; 1 ♂ 2. 8. 1935; 1 ♂ 17. 7. 1934; 1 ♂ 7. 8. 1934; 2 ♂ 3. 8. 1935; 1 ♂ 12. 7. 1934; 1 ♂ 7. 7. 1934, GS-15036 ♂-SB; 1 ♂ 17. 7. 1934, GU 137 ♂ SP; 1 ♂ 21. 7. 1934, Prep. 15378 SB and FU 160 SP; 27. 6. 1934, 1 ♀ 24. 6. 1935 with genitalia in glycerol;

Females: 1 ♀ 3. 8. 1935; 1 ♀ 8. 9. 1935; 2 ♀ 3. 7. 1934 with FU 159 SP; 1 ♀ 29. 6. 1934, GU 15063; 1 ♀ 15. 6. 1935; 1 ♀ "Li-kiang ca. 2000 m, Prov. Nord-Yuennan, 26. 6. 1934. H. Höne" with genitalia in glycerol.

Diagnosis (fig. 1, 2).- Head and body: Antenna comparatively stout in the males, pubescent. Labial palpi rather long, upcurved, terminal segment almost reaching base of antennae. Frons smoothly scaled, whitish like the palpi. Thorax and abdomen greyish-brown, mixed with white, abdominal tergites with posterior white tranverse bands.

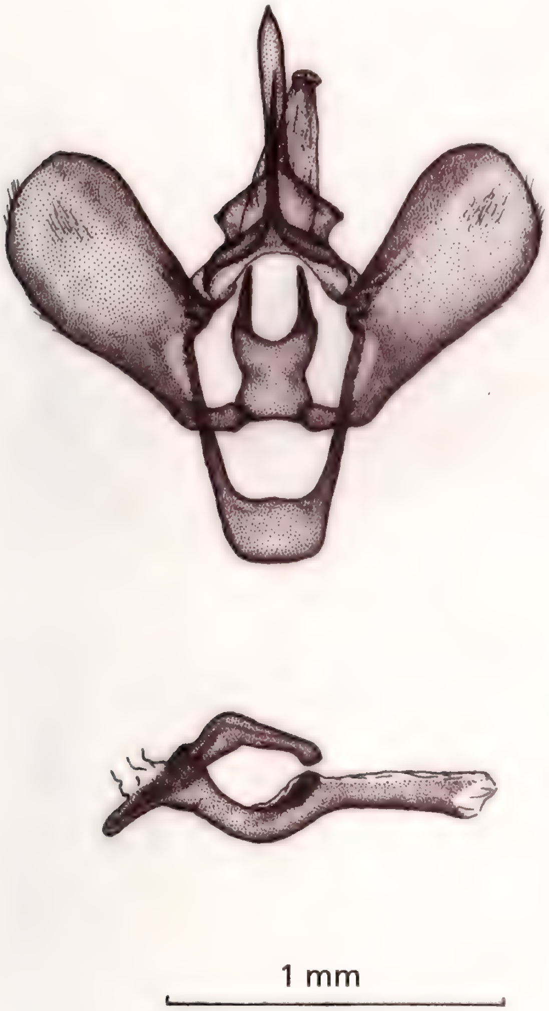


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Fig. 5: *Ambia naumanni* sp. nov., male genitalia.

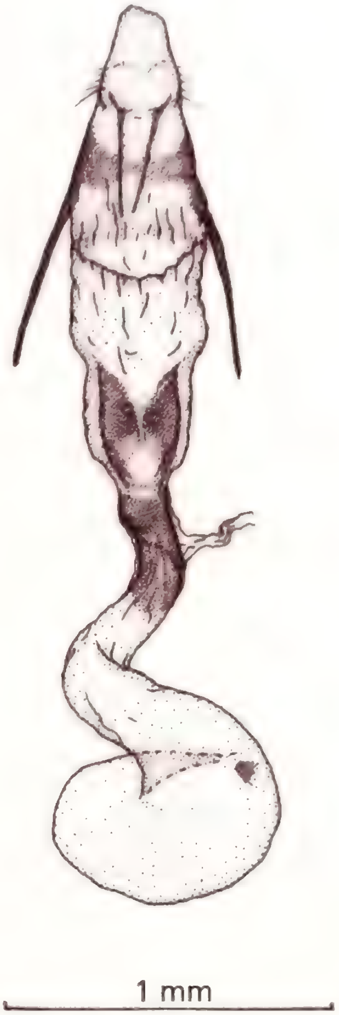

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Fig. 6: *Ambia naumanni* sp. nov., female genitalia.

Wings: Wingspan 15-17 mm, forewing length 7,5-8 mm. Wings with termen sinuous as usual in the genus, apices produced. Ground colour yellowish. Transverse fasciae prominent, white, bordered blackish-brown. The basal fascia strongly oblique, broken, the proximal one slightly curved, the distal one outcurved anteriorly and strongly retracted below middle, reaching the inner margin at about one half. The latter fascia is widened to a quadrangular spot at inner margin. Submarginal fascia conspicuous, widening towards tornus. Medial area with a white disco-cellular spot and another larger white spot in the anterior angle of the distal fascia. Marginal area yellow. Hindwing with similar pattern. Proximal fascia wider than in forewing, submarginal fascia strongly widening towards apex, incised at vein M2. Medial area suffused with brownish scales, like in the forewing, with two large white spots at the costal region and a small one at inner margin. Marginal area yellow. The venation (fig. 7) shows no principle difference to the other members of the genus.

Male genitalia (Fig. 5): Vinculum large, with u-shaped saccus. Tegumen short, uncus with a broadly triangular base, otherwise slender, distinctly flattened dorsoventrally, curved ventrad, pointed. Gnathos with strong lateral arms, medial process very narrow, slightly curved parallel to the uncus, minutely dentate dorsally, pointed at tip. Juxta large, with two dorsal spines situated laterally at the posterior margin. Valva simple, broadening towards apex, without a saccular spine or other appendages, slightly ciliate. Aedeagus with a slender, sharply bent process, arising just distally to the opening of the ductus ejaculatorius. Shaft of aedeagus strongly incurved beneath this process. A curved appendage originates at the inner side of the sinus.

Female genitalia (Fig. 6): Ovipositor comparatively short, with moderately long apophyses. Ostium wide, with a bilobed sclerotized structure inside. Upper third of the ductus bursae sclerotized, with the ductus seminalis originating in the center of this region. Ductus bursae slightly broadening towards corpus, which is small and with a trace of a signum only.

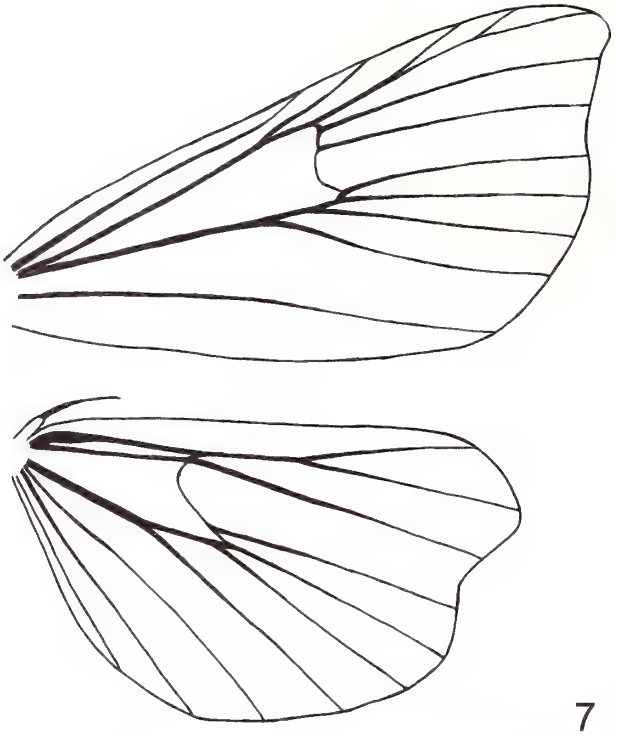

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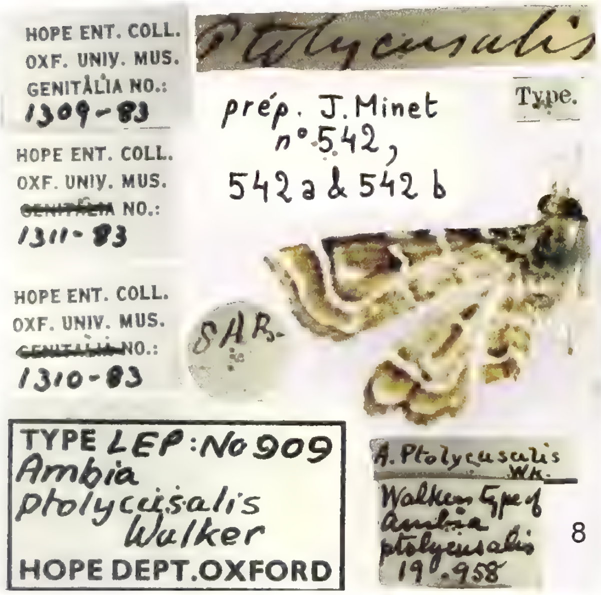
Fig. 7: *Ambia naumanni* sp. nov., wing venation.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Ptolycusalis
prép. J. Minet
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Walker
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Fig. 8: *Ambia ptolycusalis* Walker, 1859. Holotype with labels (Sarawak, Borneo).

The new species is very similar to the Western Palearctic *Ambia thyridialis* Lederer, which can easily be distinguished by the more brownish ground colour of the wing surface, with yellowish scales only found in the marginal fasciae. *Ambia thyridialis* Lederer is also similar in the male genitalia, lacking the saccular process of the valvae as well, but the aedeagus is completely different.

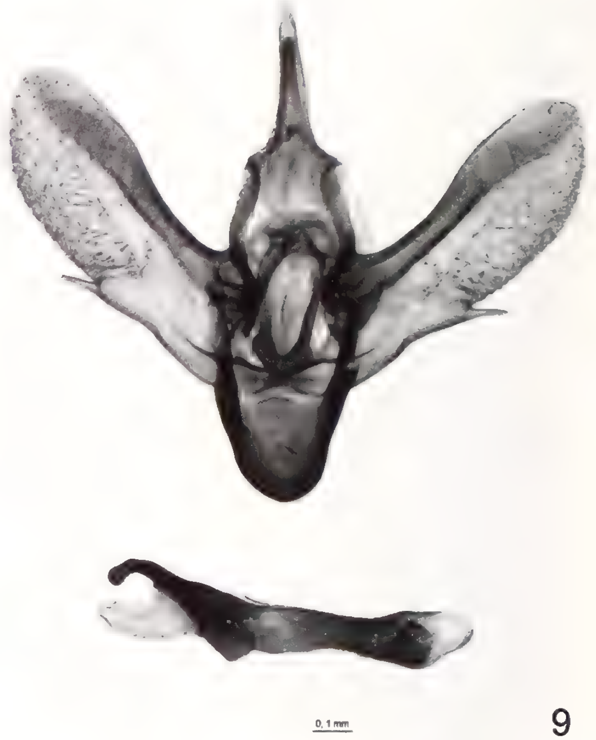

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Fig. 9: *Ambia ptolycusalis* Walker, 1859. Male genitalia of holotype.

Distribution and bionomics: Hitherto only known from the type-locality in SW. China, Yunnan, Yuelingshan near Lijiang, at elevations between 2800 and 3500 m. Flight-period from mid of June until beginning of September. First instars and foodplant unknown, but probably fern-feeding, as most of the Musotiminae are.

Acknowledgments and etymology. The new species is named in honour of Prof. Dr. C. M. NAUMANN who improved the situation in the entomological department of our museum considerably during his directorship and facilitated our work in many respects. We are grateful to Prof. Dr. K. Efetof and V. Saenko for the drawings of the genitalia and to D. J. Mann (Hope Entomological Collections, Oxford) for the loan of the type slides of *Ambia ptolycusalis*.

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Bonner zoologische Beiträge	Band 53 (2004)	Heft 1/2	Seiten 227–234	Bonn, Juni 2005

A New *Paracymoriza* Species from Lombok (Indonesia) (Lepidoptera, Crambidae)[1]

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[2)] Zoologische Staatssammlung, Munich (Germany)

Abstract. A new species *Paracymoriza naumanniella* **sp. nov**. from Lombok island is described and assigned to the *Paracymoriza albifascialis* species group. Moreover, data on the egg structure, habitat, and behaviour of the adult moths are given. In addition, DNA sequence information of mitochondrial cytochrome oxidase subunit I are furnished, which constitute the first report of genetic data concerning this gene within the family Crambidae.

Key words: Acentropinae, *Paracymoriza naumanniella* sp. nov., taxonomy, mtDNA, COI

1. INTRODUCTION

The genus *Paracymoriza* Warren, 1890 is a species rich genus within the family Crambidae, belonging to the superfamily Pyraloidea (Pyralid moths). Within the Crambidae, it is a member of the subfamily Acentropinae (former Nymphulinae, aquatic moths). In the past, *Paracymoriza* has been treated as a synonym of *Parthenodes* Guenée, 1854 which is an unrelated genus which has, in contrast, an exclusively new world distribution. *Paracymoriza* comprises 28 currently recognized species in the Oriental Region (SPEIDEL & MEY 1999; SPEIDEL 2003). The new species occurs in Lombok, Indonesia and seems to be closely associated with humid ecosystems where the specimens of the type series have been found.

2. TAXONOMY

***Paracymoriza naumanniella* sp. nov.** (Figs. 1 A, 1 B, 2 a, 2 b)

Material: Holotype ♂: "Indonesia, North Lombok, Gunung Rinjani NP, Air terjun, near village Senaru, ca. 500 - 600 m, 08°18' S / 116°24' E, 28. Dezember 2003, TF, leg. Mei-Yu Chen & Ulf Buchsbaum". "DNATAX 02820"; genitalia slide no.: M3450 Zoologische Staatssammlung München (Munich, Germany).

11 paratypes: same data, one ♀ with genitalia slide no. M3451 in Zoologische Staatssammlung München, 2 paratypes in Museum für Naturkunde, Berlin (one of them with additional label "DNATAX02824") and 2 paratypes in coll. W. Speidel, Bonn (one with additional label "DNATAX02822").

DNA is stored in the frozen DNA collection of the ZSM under storage numbers DNATAX02820 (holotype), DNATAX02821 (paratype), DNATAX02822 (paratype), DNATAX02823 (paratype), DNATAX02824 (paratype), and DNATAX02825 (paratype).

Description: Length of forewing: ♂ 9 – 11mm, ø 10 mm; ♀ 9 – 11 mm, ø 10,2 mm.

Wingspan: ♂ 17 – 22 mm, ø 17,8 mm; ♀ 19 – 23 mm, ø 21 mm.

Body dark grey, abdomen with white intersegmental rings. White ground-colour of the wings strongly reduced, therefore pattern not very contrasting.

Forewing: Inner, medial and submarginal areas dark grey, basal area almost black. Basal, proximal and distal fascia narrow, whitish. Distal fascia strongly incurved close to inner termen, with a dent directed towards the termen on vein CuP. Some marginal white spots along the termen, fringe blackish.

Hindwing: In contrast to other small *Paracymoriza* species, the wing pattern is clearly visible, though the medial area is strongly suffused like in the forewing. Basal, proximal and distal fascia narrow, whitish. The distal fascia with outwardly direced dent. Discal spot black, very close to proximal fascia.

♂ *genitalia* (Fig. 3): Valva distally rounded, elongate, reminiscent of the other members in the genus, however only with two large, acute inwardly directed, apical, setae and several smaller hairs along the distal margin. Uncus elongate, rounded towards end, gnathos slender with very inconspicuous teeth. Aedeagus comparatively strong, without cornuti, bulbus ejaculatorius arising from this center.

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[1] In commemoration of Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004)

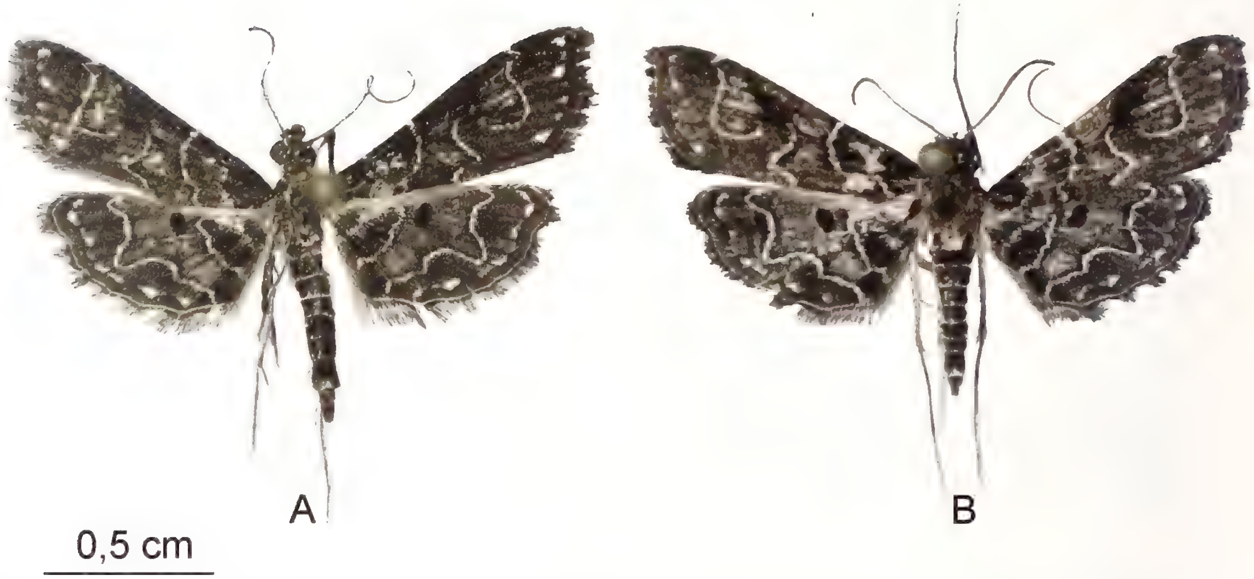

Fig. 1: *Paracymoriza naumanniella* sp. n. Holotype (male) (A) and one Paratype (female) (B). Indonesia, North Lombok, Gunung Rinjani NP, Air terjun, near village Senaru, ca. 500 - 600 m, 08°18' S / 116°24' E, 28. Dezember 2003, TF, leg. Mei-Yu Chen & Ulf Buchsbaum.

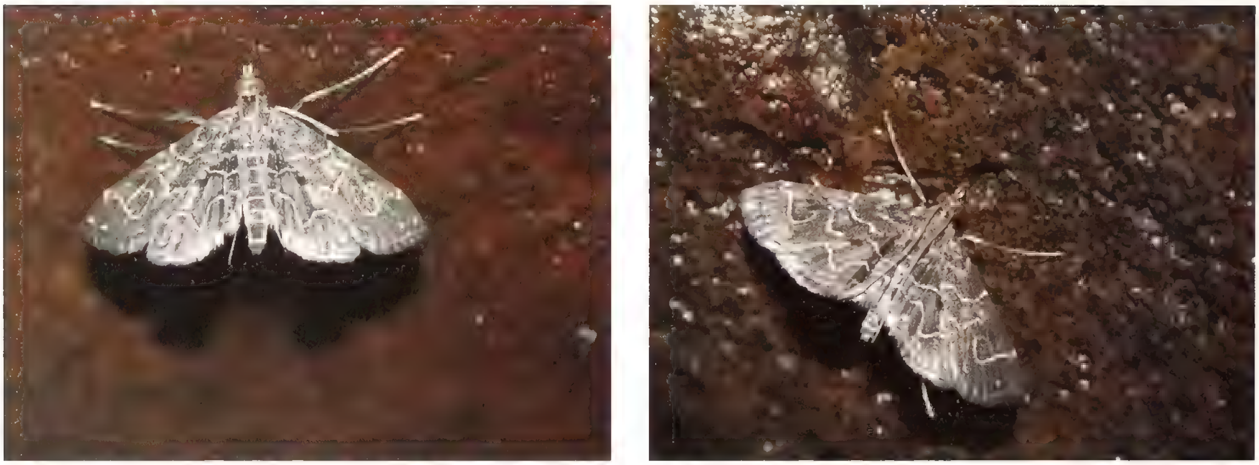

Fig. 2a-b: Paratypes of the new species still alive at the type locality in Lombok (see above). Photo: Ulf Buchsbaum.

♀ *genitalia* (Fig. 4): Ovipositor short, with long, slender, fragile apophyses. Ductus bursae rather long, gradually widening towards corpus bursae, with an unusual evagination about in its middle. Corpus bursae round, ball-shaped, without a clear signum. Colliculum situated terminally, with the slender ductus seminalis originating inside and in a short distance of the colliculum. Ostial region strongly sclerotized, large, cup-shaped, narrowing strongly towards the ductus bursae.

Egg (Fig. 7a, b): Oval, with micropylar zone at the narrow end of the egg (size: 310 x 180 µm).

Distribution (maps, Figs. 5a and 5b): Hitherto only known from the type locality in Lombok.

Genetic data: We sequenced the mitochondrial gene cytochrome oxidase subunit I in order to provide a molecular dataset for subsequent re-identification of the new species as recommended by TAUTZ et al. (2003). This gene has proven its usefulness for DNA taxonomy purposes in many studies (e.g. HEBERT et al. 2003).

Genetic characterization: *Method*: DNA was extracted from abdominal tissue of some of the type specimens of *P. naumanniella* sp. nov. using Qiagen (Hilden, Germany) tissue kit according to the protocol of KNÖLKE et al. (2005). Mitochondrial (mtDNA) cytochrome oxidase subunit I (COI) gene was amplified with PCR using protocols and primers as in SIMON et al. (1994). Direct sequencing of dye labelled templates was carried

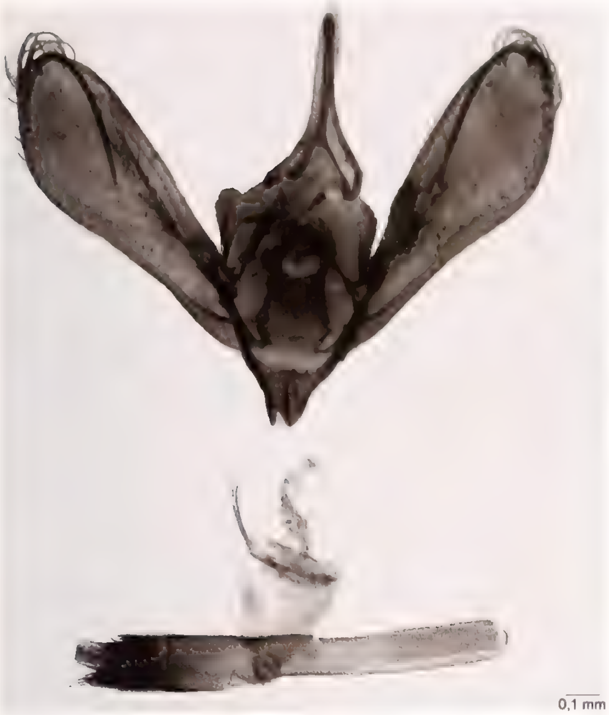

Fig. 3: Holotype male genitalia.

out using an ABI 377 automated sequencer (Applied Biosystems). Up to 10 single sequences per individual were assembled and aligned to the COI gene of *Bombyx mori* (L., 1758) (Lepidoptera, Bombycidae; GenBank accession number NC_002355).

Result: The following sequence of *P. naumanniella* sp. nov. shows the partial COI gene of the holotype:

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>Paracymoriza_naumanniella_Holotype_
DNATAX02820_1230bp

CGAAAATGACTTTATTCTACAAATCATAAAGAT
ATTGGAACTTTATATTTTATTTTTGGAATTTGAT
CGGGAATAGTTGGAACATCTTTAAGATTATTAA
TTCGAGCTGAATTAGGAAATCCTGGATCATTAA
TTGGAGATGATCAAATTTATAATACTATTGTTA
CTGCTCATGCTTTTATTATAATTTTTTTTATAGT
AATGCCAATTATAATTGGAGGATTTGGAAATTG
ATTAGTTCCATTAATATTAGGTGCTCCTGATAT
GGCTTTCCCACGAATAAATAATATAAGATTTTG
ACTTCTTCCTCCATCTCTTACACTTTTAATTTCA
AGAAGAATCGTAGAAAATGGAGCAGGAACAGG
ATGAACAGTGTACCCCCCACTATCATCTAATAT
CGCTCATGGAGGAAGATCTGTAGATTTAGCTAT
TTTTTCCTTACATTTAGCTGGTATTTCCTCAATT
TTAGGAGCAATTAATTTCATTACTACAATTATT
AACATACGAATTAATAATTTATTTTTTGATCAA
ATACCTCTTTTTATTTGAGCGGTAGGTATTACA
GCTTTACTTCTTCTTCTTTCTTTACCAGTTTTAGC
TGGAGCAATTACTATGTTATTAACAGATCGAAA
TTTAAATACATCTTTTTTTGATCCTGCTGGAGGA
GGAGATCCAATTTTATATCAACATTTATTTTGAT
TTTTTGGGCATCCCGAAGTATATATTTTAATTTT
ACCAGGATTTGGAATAATCTCTCATATTATTTCT
CAAGAAAGAGGAAAAAAAGAAACTTTTGGATC
TTTAGGAATAATTTATGCTATAATAGCAATTGG
ATTATTAGGATTTGTTGTTTGAGCACATCATAT
ATTTACTGTAGGTATAGATATTGATACTCGAGC
ATATTTTACTTCTGCAACTATAATTATTGCTGTA
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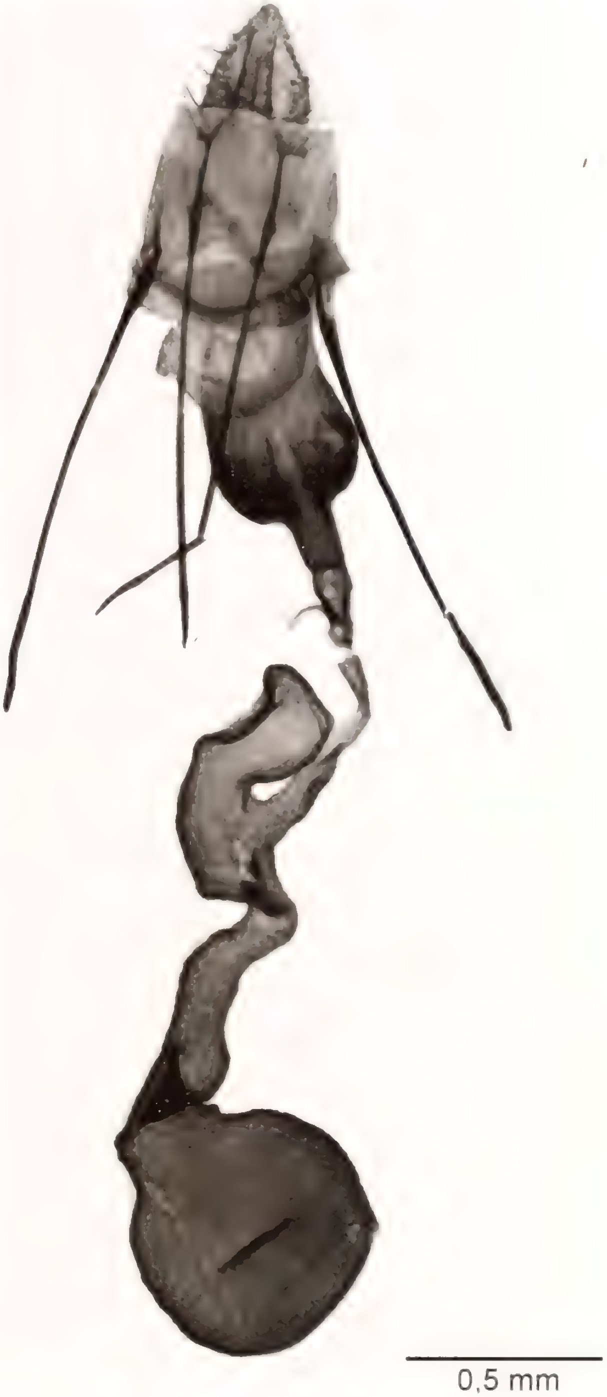


Fig. 4: Paratype female genitalia.

CCAACAGGAATTAAAATTTTTAGATGATTAGCA
ACCTTACATGGAACTCAAATTAATTATAGACCT
TCTACTTTATGAAGATTAGGATTTGTATTTTTAT
TTACTGTAGGGGGATTAACTGGAGTTGTTTTAG
CTAATTCTTCAATTGATGTAGCTCTTCATGATAC
TTATTATGTAGTAGCACATTTTCATTATGTTCTA
TCTATAGGAGCAGTATTTGCTATTTTAGGAGGT
TTTATTCATTGATATCCATTATTTACAGGATTAACTCTTAAACCTTATTACTTAAAAATTCAA

The complete COI gene of the paratypes is shown for DNATAX02821:

>Paracymoriza_naumanniella_Paratype_
DNATAX02821_1530bp

CGAAAATGACTTTATTCTACAAATCATAAAGATA
TTGGAACTTTATATTTTATTTTTGGAATTTGATCG
GGAATAGTTGGAACATCTTTAAGATTATTAATTC
GAGCTGAATTAGGAAATCCTGGATCATTAATTGG
AGATGATCAAATTTATAATACTATTGTTACTGCT
CATGCTTTTATTATAATTTTTTTTATAGTAATGCC
AATTATAATTGGAGGATTTGGAAATTGATTAGTT
CCATTAATATTAGGTGCTCCTGATATGGCTTTCCC
ACGAATAAATAATATAAGATTTTGACTTCTTCCT
CCATCTCTTACACTTTTAATTTCAAGAAGAATCG
TAGAAAATGGAGCAGGAACAGGATGAACAGTGT
ACCCCCCACTATCATCTAATATCGCTCATGGAGG
AAGATCTGTAGATTTAGCTATTTTTTCCTTACATT
TAGCTGGTATTTCCTCAATTTTAGGAGCAATTAA
TTTCATTACTACAATTATTAACATACGAATTAAT
AATTTATTTTTTGATCAAATACCTCTTTTTATTTG
AGCGGTAGGTATTACAGCTTTACTTCTTCTTCTTT
CTTTACCAGTTTTAGCTGGAGCAATTACTATGTT
ATTAACAGATCGAAATTTAAATACATCTTTTTTT
GATCCTGCTGGAGGAGGAGATCCAATTTTATATC
AACATTTATTTTGATTTTTTGGGCATCCCGAAGTA
TATATTTTAATTTTACCAGGATTTGGAATAATCTC
TCATATTATTTCTCAAGAAAGAGGAAAAAAAGA
AACTTTTGGATCTTTAGGAATAATTTATGCTATA
ATAGCAATTGGATTATTAGGATTTGTTGTTTGAG
CACATCATATATTTACTGTAGGTATAGATATTGA
TACTCGAGCATATTTTACTTCTGCAACTATAATTA
TTGCTGTACCAACAGGAATTAAAATTTTTAGATG
ATTAGCAACCTTACATGGAACTCAAATTAATTAT
AGACCTTCTACTTTATGAAGATTAGGATTTGTAT
TTTTATTTACTGTAGGGGGATTAACTGGAGTTGT
TTTAGCTAATTCTTCAATTGATGTAGCTCTTCATG
ATACTTATTATGTAGTAGCACATTTTCATTATGTT
CTATCTATAGGAGCAGTATTTGCTATTTTAGGAG
GTTTTATTCATTGATATCCATTATTTACAGGATTA
ACTCTTAAACCTTATTACTTAAAAATTCAATTTAT
TACAATATTTATTGGAGTAAATTTAACTTTTTTCC
CACAACATTTTTTAGGTTTAGCTGGAATACCACG
ACGATATTCTGATTATCCTGACATTTATATTTCAT
GAAATATTATTTCTTCATTAGGATCTTATATTTCA
TTATTAGCAATTATAATAATAATAATAATTATTT
GAGAATCAATAATTAACCAACGAATTATTTTATT
TTCATTAAATTTATCATCTTCTATTGAATGATATC
AAAATTTACCCCCTGCAGAACATTCATATAATGAACTTCCTATTTTAAGAAAT

Species variation: In addition to the holotype we sequenced four of the paratypes. The sequence variation within the set of types is shown in Table 1. There are six variable sites within the complete sequences of COI of the paratypes and five variable sites within all type specimens due to the reduced sequence lengths available for comparison (1.230bp). Therefore the species variation is 0.39% sequence divergence within the complete gene and 0.41% in the short dataset.

Table 1: Variable sites and positions.
Abbreviation: n.a. - sequence data not available.

varable sites: positions COI	69	309	351	708	1113	1283
DNATAX02820 (holotype)	G	T	T	G	A	n.a.
DNATAX02821 (paratype)	G	T	T	G	A	T
DNATAX02823 (paratype)	G	T	T	G	A	G
DNATAX02824 (paratype)	A	C	C	A	G	T
DNATAX02825 (paratype)	G	T	T	G	A	T

The new sequences are deposited under the accession numbers AJ 852519 (DNATAX02820, holotype), AJ 852520 (DNATAX02821, paratype), AJ 852521 (DNATAX02823, paratype), AJ 852522 (DNATAX 02824, paratype), and AJ 852523 (DNATAX02825, paratype), respectively, at EBI/GenBank.

Remarks on the molecular studies. The aim is to provide an additional character set in the diagnosis of the new species. There is at the moment no possibility to include related species in a differential diagnosis on DNA sequence level due to the missing COI data of other species of the family Crambidae.

Biological data: The imagines of the new species are so far found only in December. The biotope is a primary rain forest, near a waterfall, with very high humidity due to the mist.

The moths rest on the algae covered sides of stones and rocks situated close to or in the water. Eventually they jump onto the surface of the water and afterwards back to the rock. The moth are highly hydrophobic, can be completely submerged under waves, but are not trapped by the surface-tension of the water. They seem to be very connected to their restricted habitat and to leave it very rarely and only within little distances.

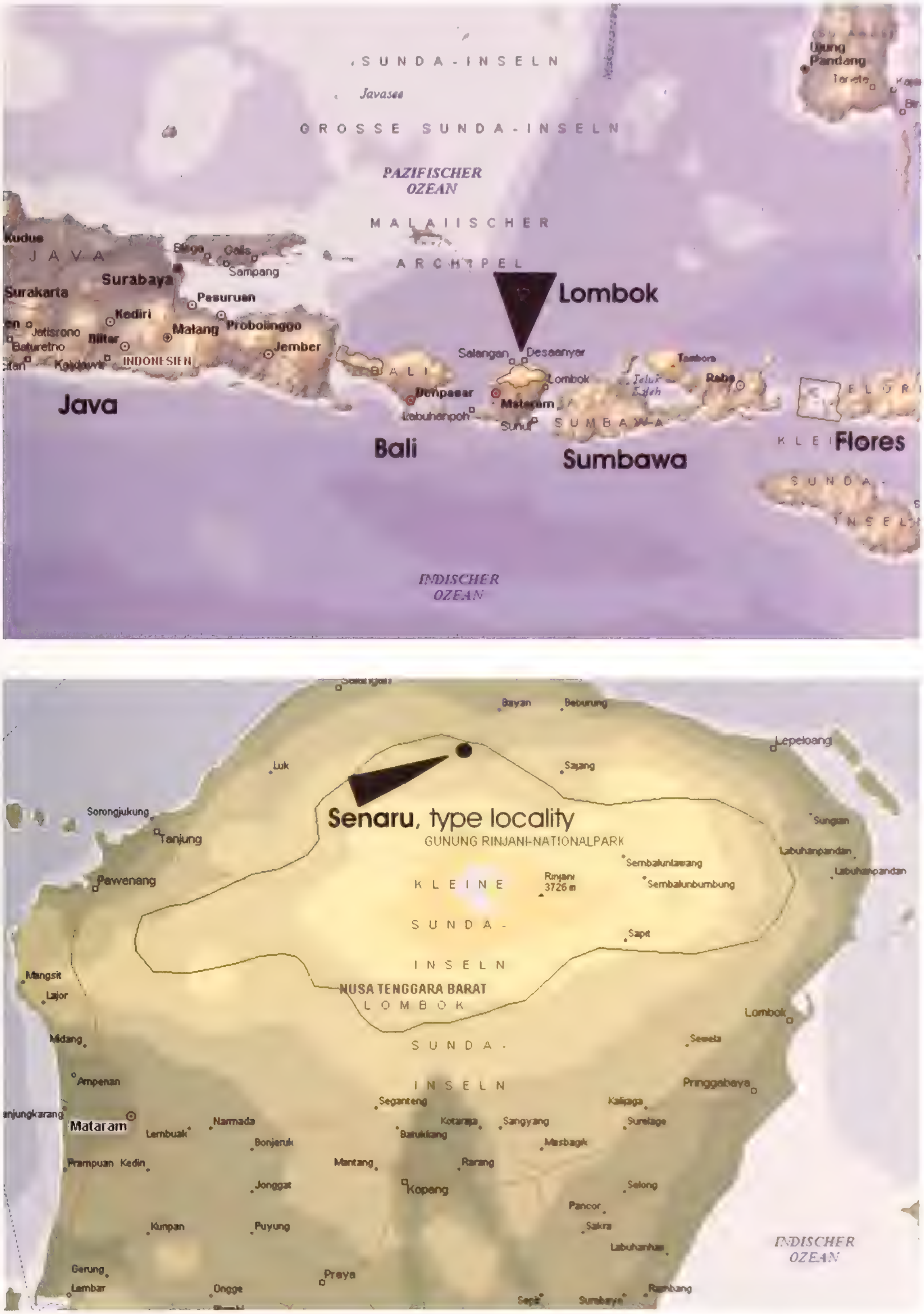
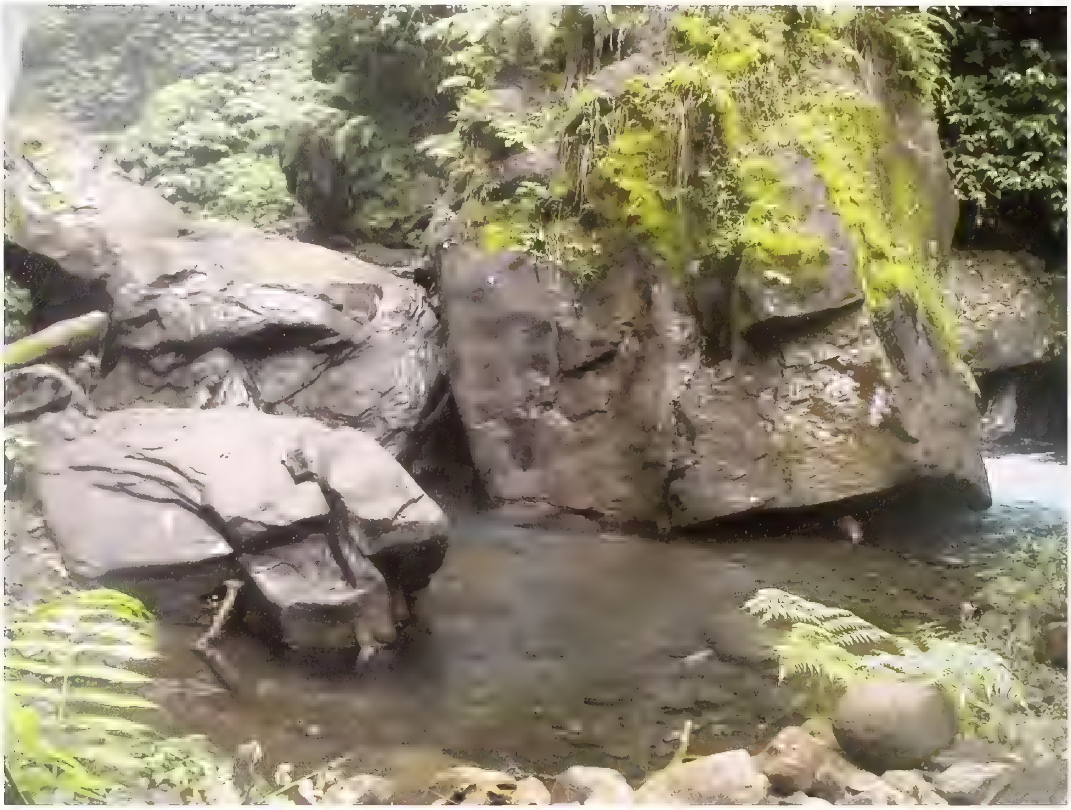

SUNDA-INSELN
Javasee
GROSSE SUNDA-INSELN
PAZIFISCHER OZEAN
MALAIISCHER ARCHIPEL
Lombok
JAVA
Kudus
Surabaya
Surakarta
Sampang
Pesuruan
Kediri
Malang
Probolinggo
Jember
Blitar
INDONESIEN
Java
BALI
Denpasar
Bali
Selangan
Desaenyar
Mataram
SUMBAWA
Sumbawa
Teluk Saleh
Tambora
Raba
Flores
KLEINE
SUNDA-INSELN
Ujung Pandang
INDISCHER OZEAN
Bayan
Beburung
Lepeloang
Luk
Sajang
Senaru, type locality
GUNUNG RINJANI-NATIONALPARK
Sorongjukung
Tanjung
Pawenang
Sembalunlawang
Sembalunbumbung
Rinjani 3726 m
KLEINE
SUNDA-
INSELN
Sapit
NUSA TENGGARA BARAT
LOMBOK
Lombok
Mangsit
Lajor
Midang
Sewela
SUNDA-
INSELN
Ampenan
Pringgabaya
Seganteng
Kalipaga
Mataram
Narmada
Lembuak
Kotaraja
Sangyang
Suralaga
Bonjeruk
Barukijang
Masbagik
Prampuan
Kedin
Mantang
Rarang
Jonggat
Kopang
Selong
Pancor
Sakra
Kunpan
Puyung
Labuhanhaji
Gerung
Lembar
Praya
Ongge
Rambang
INDISCHER OZEAN

Fig 5: Type locality. 5 a: Enlarged view to show the situation of the Island Lombok (Indonesia) east of Bali; 5 b: type locality of *P. naumanniella* on Lombok Island near the village Senaru below the mountain Gunung Rinjani.



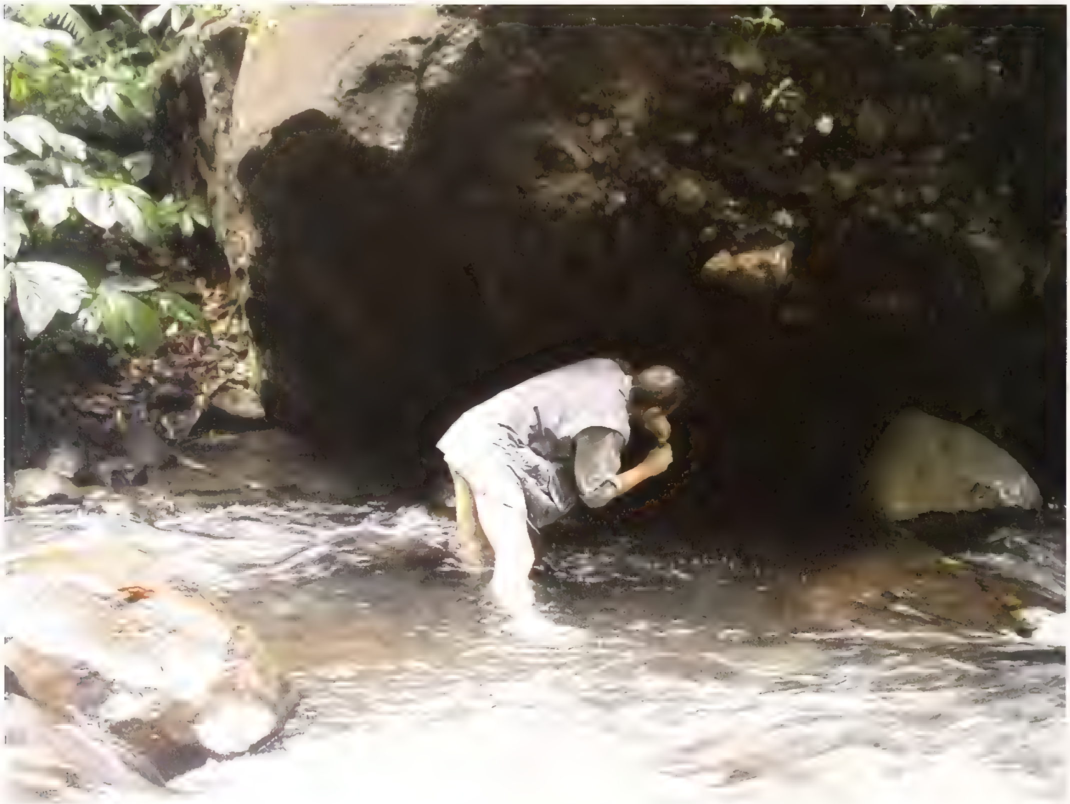


Fig. 6: Biotope at type locality beside the waterfall. 6 a: Here, most moths rest under the rocks near the water surface. Photo: Ulf Buchsbaum; 6 b: One of the authors (U. B.) collecting specimens of the new species. Photo: Mei-Yu Chen.

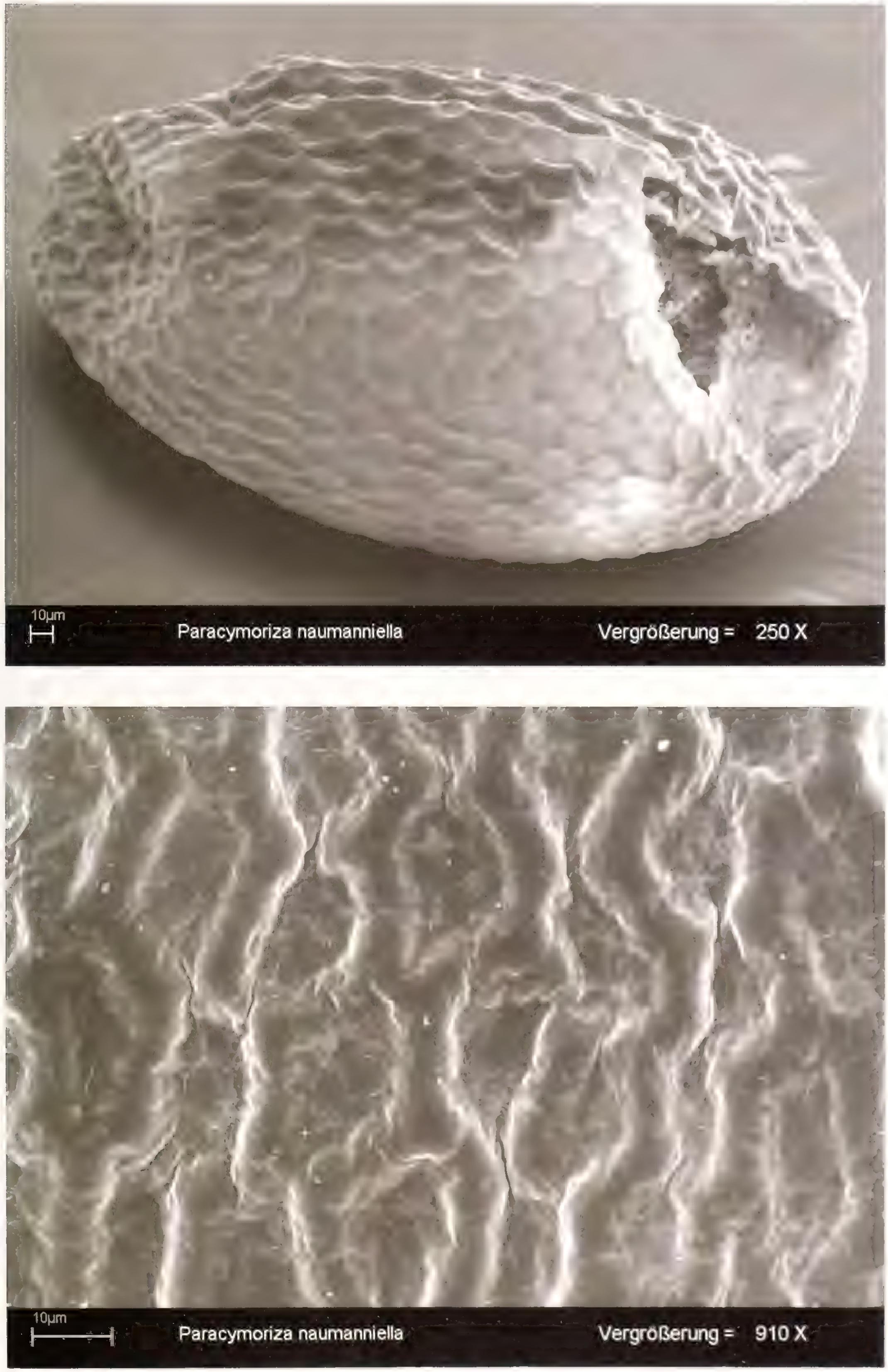

10µm
Paracymoriza naumanniella
Vergrößerung = 250 X
10µm
Paracymoriza naumanniella
Vergrößerung = 910 X

Fig. 7: SEM photos of the egg of *Paracymoriza naumanniella*. 7 a: Egg (total view); 7 b: surface structure of the egg with larger magnification.

Relationships: The closest relatives of the new species can only be ascertained after a revision of the genus. A similar wing-pattern is found in the *P. albifascialis* Hampson, 1891 species group (SPEIDEL & MEY 1999), especially in the strongly toothed distal fascia. It is therefore tentatively placed in this species group, but differs from all other members of the group by the infuscated medial area of both wing-pairs and the small size. Differences from the *Paracymoriza distinctalis* (Leech, 1889) group include the slender wing-shape (broader in the *P. distinctalis* species group) and the size (larger in the *P. distinctalis* species group). Members of the *P. nigra* (Warren, 1896) species group show the same small size, however the pattern is almost absent from the hindwing.

Etymology: The species is named in honour of the late Prof. Dr Clas M. NAUMANN, one of the most important contemporary lepidopterists who has successfully introduced and used the methods of Phylogenetic Systematics in lepidopterology.

3. DISCUSSION

The approach to include genetic data in new species descriptions is facing more and more acceptance within the scientific community. Proponents of the so-called 'DNA taxonomy' plea for the use of genetic markers as a unique determination tool (TAUTZ et al. 2003). The question which gene to use is tending to the well investigated COI gene of the mitochondrion (HEBERT et al. 2003). Critics of the choice refer to the risk of misleading results due to the analysis of paralogous sequences because of independent evolving nuclear insertions of mitochondrial genes (THALMANN et al. 2004). Nevertheless these rare exceptions should not keep taxonomists from producing genetic markers of newly described species. There is a major chance in the offering of genetic markers: Unknown immature stages can easily be associated with adult descriptions. Breeding of aquatic moths in the field is rather difficult and in the present case the early stages of *P. naumanniella* sp. nov. are unknown. The genetic data will enable to associate larvae in the future. The new species may have aquatic larvae, which probably live in the current water of small creeks close to the locations where the imagines were found. The assignment of unknown larvae to the species they belong, is only possible by analysis of their genome when rearing of the caterpillars is not feasible. Prof. Dr. Clas M. NAUMANN had been aware of the chances genetic markers offer for taxonomy. In his late years he hardly hesitated to become a proponent of DNA taxonomy, and his main focus still laid on the phylogenetic aspect which genetic information of taxa provides.

Acknowledgements. We thank Dr Axel Hausmann (Munich) for his discussion about the manuscript. We are grateful to Mei-Yu Chen (Meifeng, Taiwan) for her help in the field-work and photographic assistance and Dr. Wolfram Mey (Berlin) kindly allowed the use of the large reference collection in the Museum für Naturkunde, which is especially rich in South East Asian material. Special thanks also to Enrico Schwabe (Munich) for his kind help with SEM photos.

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Bonner zoologische Beiträge | Band 53 (2004) | Heft 1/2 | Seiten 235–254 | Bonn, Juni 2005

Adult Morphology and the Higher Classification of *Bia* Hübner (Lepidoptera: Nymphalidae) [1]

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Abstract. The South American nymphalid *Bia* Hübner, 1819, treated for over 150 years by most lepidopterists as a member of the Satyrinae, has been shown by recent work on early stages and DNA to share characters with the Morphinae: Brassolini. Examination of the wing patterns and androconial organs of *Bia*, described in detail for the first time, reveals unusual features otherwise only known from brassolines. In particular, the tufted posterior androconial organ of the hindwing forming palisades is a synapomorphy for *Bia* and several genera of Brassolini, including *Caligo*. The genus *Bia* is formally transferred from the Satyrinae to the Morphinae: Brassolini as the sole member of the subtribe Biina Herrich-Schäffer, 1864, **stat. nov.**, co-ordinate with Brassolina Boisduval, 1836, and Naropina Stichel, 1925.

Key words. Systematics, Satyrinae, Morphinae, Brassolini, *Caligo*, androconia, Neotropics, butterflies

> *The brothers Kratos and Zelos, and their sisters Nike and Bia, were the personifications of strength, rivalry, victory and force. These four winged gods stood beside the throne of Zeus*
> http://www.theoi.com/Ouranos/Kratos.html

1. INTRODUCTION

The genus *Bia* Hübner, 1819, has long been a puzzle to systematists. At present only one species is recognised, *Bia actorion* (Linnaeus, 1763). However, our investigations and those of Gerardo LAMAS (pers. comm., Lima 2004) indicate that there may be two or more sibling species, and this will be addressed in a future paper (LAMAS, BOPPRÉ, HOARE & VANE-WRIGHT in prep.).

In general facies *Bia* is markedly divergent from other butterflies, and both sexes are instantly recognisable as members of the genus (Figs 1–4). The butterflies are restricted to lowland and lower-montane forests of South America, occurring in dense undergrowth where the canopy is not fully closed. Individuals fly along trails and in clearings in damp, marshy areas, and are active from dawn to dusk. They often settle on rotting fruits, on which they feed, or on vegetation about a metre above the ground, when they may reveal their yellowish and blue upper side pattern. Mark and recapture studies indicate that males can live for at least 20 days, and are generally loyal to a particular patch of forest. In flight, the iridescent blue patches sported by most individuals flash conspicuously. If threatened, the butterflies dash into the base of a bush, where they are very difficult to reach. As they settle after an escape flight, the wings are closed to reveal only the cryptic, ripple-pattern underside (Fig. 5). This, together with the sudden disappearance of the distinctive blue colour, makes them difficult to locate. Interactions between males are frequent, and courtship is lengthy and complex, including tandem flight patterns, contact during flight, and male flight over perched females that apparently may respond by flashing their wings. Until very recently their early stages and host plants were unknown (BARTLETT 1876; HALL 1939; MASTERS 1970; FREITAS et al. 2002; Keith WILLMOTT, pers. comm., London 2004).

Bia adults have tri-carinate antennae and small forelegs in both sexes, and the genus undoubtedly belongs to the Nymphalidae *sensu* ACKERY et al. (1999). Its systematic position within the family has, however, been very uncertain. With no convincing evidence to support MILLER's (1968) suggestion of a relationship to the melanitine Satyrinae, D'ABRERA (1988: 846; 2001: 340), for example, has continued to locate *Bia* amongst the Pronophilina, the dominant group of typical Satyrinae found in mountainous regions of South America. This reflects a convention first adopted by KIRBY (1871) in his 'Catalogue', and subsequently followed by WEYMER (1911: 276) in 'Seitz', and by GAEDE (1931: 524) in 'Lep. Cat.'. MIELKE & CASAGRANDE (1998) list the Biini immediately after the Pronophilini.

FREITAS & BROWN (2004), in contrast, conclude that *Bia* should be placed as a monobasic subfamily (Biinae) within their "satyroid clade", reflecting a view going back to HERRICH-SCHÄFFER (1864) that gives *Bia* very high taxonomic rank. In most of their analyses, *Bia* appeared in various relationships with the Satyrinae, Mor-

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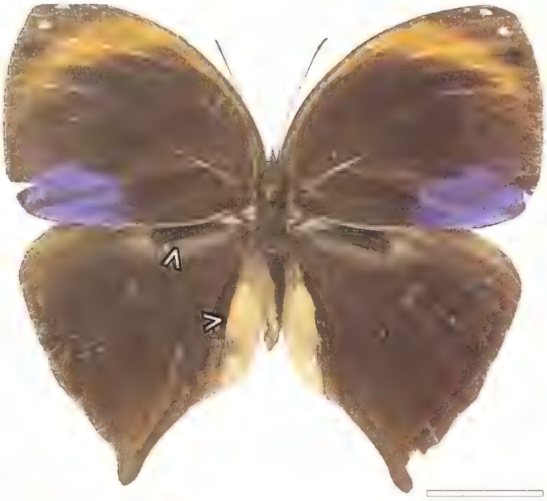
[1] In commemoration of Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004)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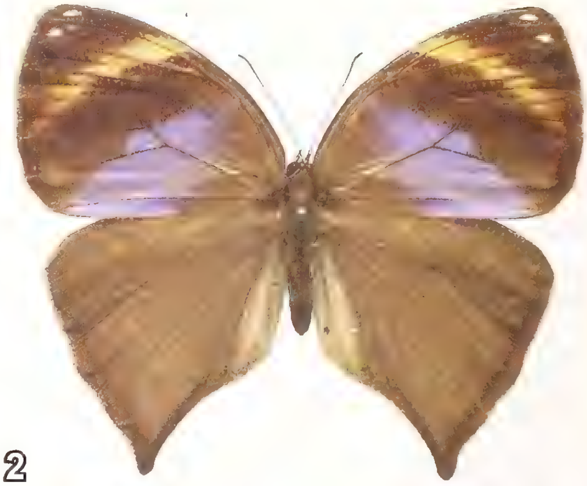
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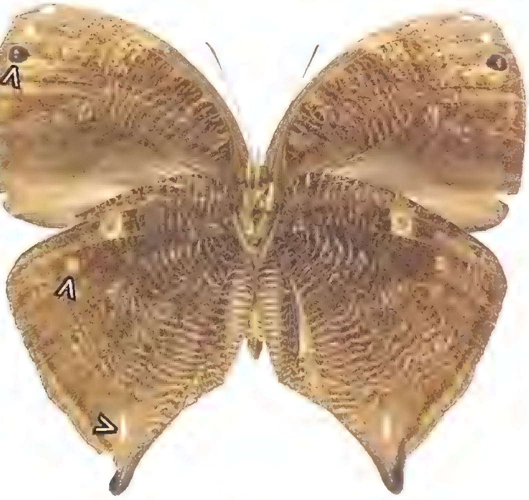
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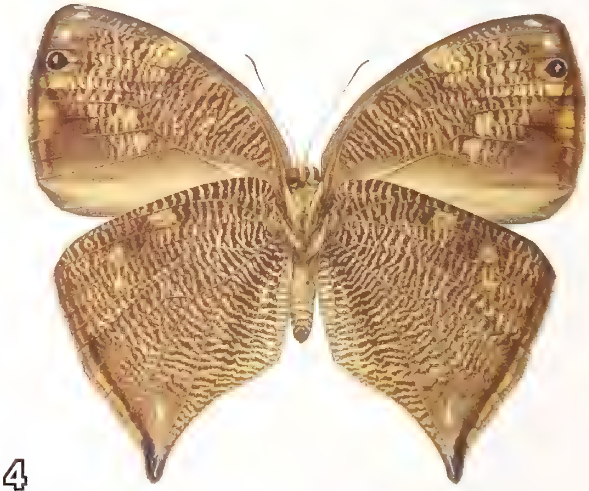
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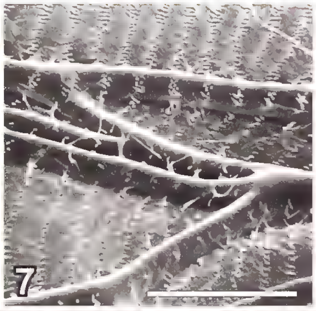
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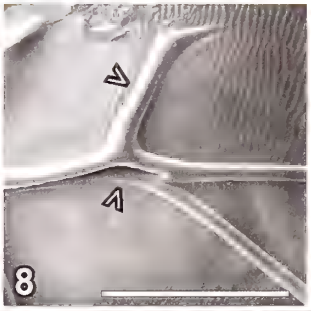
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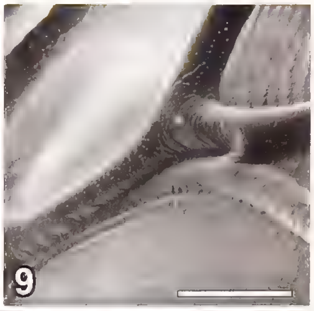
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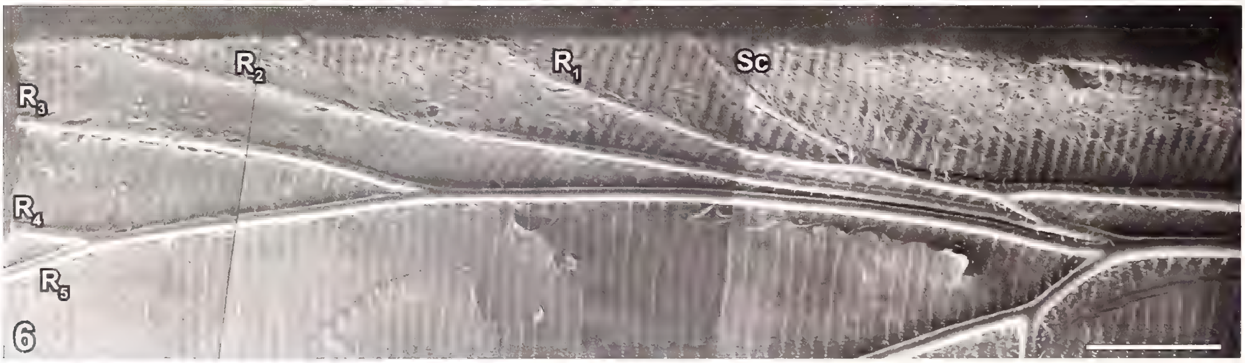
6
R2
R1
Sc
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phini, Brassolini and Calinaginae, although in a successive weightings analysis it appeared as the stem group of the Brassolini (FREITAS & BROWN 2004: fig. 2). Recent publications by BROWER (2000) and FREITAS et al. (2002) have provided, respectively, valuable new data on the molecular systematics and early stages that are consistent with the idea that *Bia* is a member of the Brassolini, one of the two South American tribes that belong to the Morphinae. This view, that *Bia* is a brassoline, was first put forward by CLARK (1947), tentatively supported by DEVRIES et al. (1985), and recently accepted by YOSHIMOTO (2003).

Here we re-investigate the adult morphology of *Bia* and question why its membership of the Brassolini was not recognised previously. CLARK (1947, 1948) failed to provide any evidence, and inaccurate or incomplete subsequent work has obscured its natural relationships. The peculiarities of the androconial systems reported here demonstrate that, even without the evidence now available from knowledge of DNA sequences and early stage morphology, the clear relationship of *Bia* to the owl butterflies (*Caligo* Hübner, 1819) and other Brassolini has literally been "staring us in the face" for over 200 years.

2. SYSTEMATIC HISTORY

LINNAEUS (1763a,b) described *Papilio actorion* from "Indiis", for which HÜBNER (1819: 51) introduced the genus *Bia*, with *Papilio actoriaena* Hübner, 1819 (an objective synonym of *Papilio actorion*: HEMMING 1964), as the only included species. GODART (1824: 446), however, consigned *P. actorion* to *Morpho* Fabricius, 1807, in which he also included many species now placed in the Amathusiini and Brassolini.

In his outstanding contribution to *The Genera of Diurnal Lepidoptera*, WESTWOOD (1850: 321) accepted Hübner's genus for *actorion*, noting *Bia* as a "very interesting … butterfly" belonging to the "Nymphalidae". It must be appreciated, however, that Westwood's classification of the Nymphalidae differed significantly from current practice. He likened *Bia* not only to various butterflies in the "Satyridae", but in particular among his "Nymphalidae" to such genera as *Siderone* Hübner, 1823 (now in Charaxinae), *Heteropsis* Westwood, 1850 (now Satyrinae), *Kallima* Doubleday, 1849 (Nymphalinae) and *Amathusia* Fabricius, 1807, *Zeuxidia* Hübner, 1826, and *Discophora* Boisduval, 1836 (Morphinae: Amathusiini).

In contrast, HERRICH-SCHÄFFER (1864) suggested that *Bia* should have very high taxonomic rank, placing it as the sole member of a new family, the Biidae [as "Biina"], one of just 16 family groups into which he divided the entire Rhopalocera. In so doing, he compared *Bia* with butterflies now placed in the Brassolini and Danaini, but not the Satyrinae.

As noted by WESTWOOD (1850), *Bia* has the bases of forewing veins Sc, Cu and 2A conspicuously inflated. This apparently persuaded WALLACE (1854) to place *Bia* in the Satyridae: "the beautiful *Bia Actorion*, which, though classified with the Nymphalidae, exactly agrees with this family [Satyridae] in its haunts and mode of flight … [and] in many structural points." Wallace concluded that it formed "a very satisfactory link connecting the two families." In assigning *Bia* to the satyrines, he has been followed by a majority of lepidopterists ever since – e.g. FELDER (1861), DIETRICH (1862), KIRBY (1871), DRUCE (1876), MÜLLER (1877), STAUDINGER (1888), SCHATZ & RÖBER (1889), WEYMER & MAASSEN (1890), WEYMER (1911), GAEDE (1931), HALL (1939), EHRLICH (1958), HAYWARD (1958, 1964), FORSTER (1964), MILLER (1968), D'ABRERA (1988, 2001), HARVEY (1991), MIELKE & CASAGRANDI (1998), RACHELI & RACHELI (2001). However, at least two authors before the recent period linked this curious little butterfly firmly with the Morphinae – but in different ways.

REUTER (1896), in his remarkable but often neglected thesis, placed *Bia* in the Morphinae, as one of three tribes: Morphini, Amathusiini and Biini (GODART 1824, by including *actorion* as a discrete subgroup "IIA" within *Morpho*, set a precedent for this). REUTER separated the Morphinae from the Brassolini, including the latter within the much larger Satyrinae. On the other hand, and possibly taking a lead from HERRICH-SCHÄFFER, CLARK (1947, 1948) unhesitatingly placed *Bia* as a brassolid, but without giving any reason. Frustratingly, in the first of these two papers, CLARK stated confidently but without explanation, "Brassolidae [are] easily recognisable by adult characters"; no justification at all was given in his second paper. For various reasons, both REUTER (1896, 1898) and CLARK (1947, 1948) have largely been ignored.

Figs 1–9: *Bia actorion* (L.) *sensu lato*. Adult butterflies and wing venation (both specimens from Suapure, Venezuela). **1** male upperside (upper arrow: anterior alar organ; lower arrow: posterior alar organ; BMNH(E) #693091); **2** female upperside (BMNH(E) #693105); **3** underside of 1 (upper arrow: border ocellus in forewing cell M_1; mid arrow: border ocellus in hindwing cell R_5; lower arrow: border ocellus/diagonal white stripe in hindwing cell Cu_{1a}); **4** underside of **2**; **5** live individual at rest (Venezuela, Bolivar State, Jasper Falls 27.x.2000); **6** forewing radial venation from anterior apex of discal cell to separation of R_4 and R_5 (subcostal and radial veins labelled; BMNH electron micrographs #E3/273–5, composite SEM); **7** detail of 6 to show origin of radial veins from discal cell; **8** hindwing precostal area (upper arrow: precostal vein; lower arrow: precostal cell; BMNH electron micrograph #E3/270, SEM); **9** detail of 8 (BMNH electron micrograph #E3/271). Scale bars: 1–4: 10 mm; 6: 1 mm; 7: 0.5 mm; 8–9: 1 mm.

MILLER (1968) followed conventional wisdom in accepting *Bia* as a member of the Satyridae (he regarded them as a family) in which, like Reuter, he also included the Brassolini but not Morphini or Amathusiini. MILLER used the name Biinae to designate one of seven subfamily divisions for the group, and further subdivided the Biinae into three named tribes: the Melanitini, Antirrheini, and the monobasic Biini, commenting that "*Bia* is far too aberrant to be referred to either of the other two biine tribes." He also suggested that "within the Satyridae the brassolines are allied to the New World Biinae, particularly through such genera as *Narope* [Brassolini]" (MILLER 1968: 23).

Miller thus united *Bia* with the new world Antirrheini (*Antirrhea* Hübner, 1822, and *Caerois* Hübner, 1819), and the old-world Melanitini: *Melanitis* Fabricius, 1807, *Cyllogenes* Butler, 1868, *Gnophodes* Westwood, 1851, *Parantirrhoea* Wood-Mason, 1880, and *Bletogona* C. & R. Felder, 1867 (for placement of this last genus, see UÉMURA 1987). In addition, but in a very ambiguous manner, Miller also listed *Manataria* Kirby, 1908, at the end of his account of the Biinae. This peculiar genus represents a small group of South American brown butterflies of very uncertain affinity that he likened to the old world Elymniini: Lethina, as well as some members of his Biinae. In contrast, FORSTER (1964; see also RACHELI & RACHELI 2001) had earlier placed *Manataria* within the Satyrini: Euptychiina, the dominant group of lowland Satyrinae found in Latin America. MIELKE & CASAGRANDE (1998) understandably listed *Manataria* at the end of the Satyrinae as "tribe uncertain".

VANE-WRIGHT (1972a) recognised that the three higher taxa linked within the Biinae by MILLER (1968) represent an unnatural assemblage. Based on evidence from eggs, larvae and adults, DEVRIES et al. (1985) formally transferred the Antirrheini to the Morphini, as a subtribe. They also suggested that *Bia*, mainly on the evidence of its external abdominal androconia similar to those found in *Caligo* and related genera, might belong to the Brassolini, and these views were echoed by ACKERY (1984: 16, 1988: 104). In BROWER's (2000) molecular investigation, *Bia* grouped with *Caligo*, and these two genera then grouped with *Opsiphanes* Doubleday, 1849, a result consistent with CLARK's assertion and the suggestion of DEVRIES et al. This contention is further supported by the work of FREITAS et al. (2002) on the early stages.

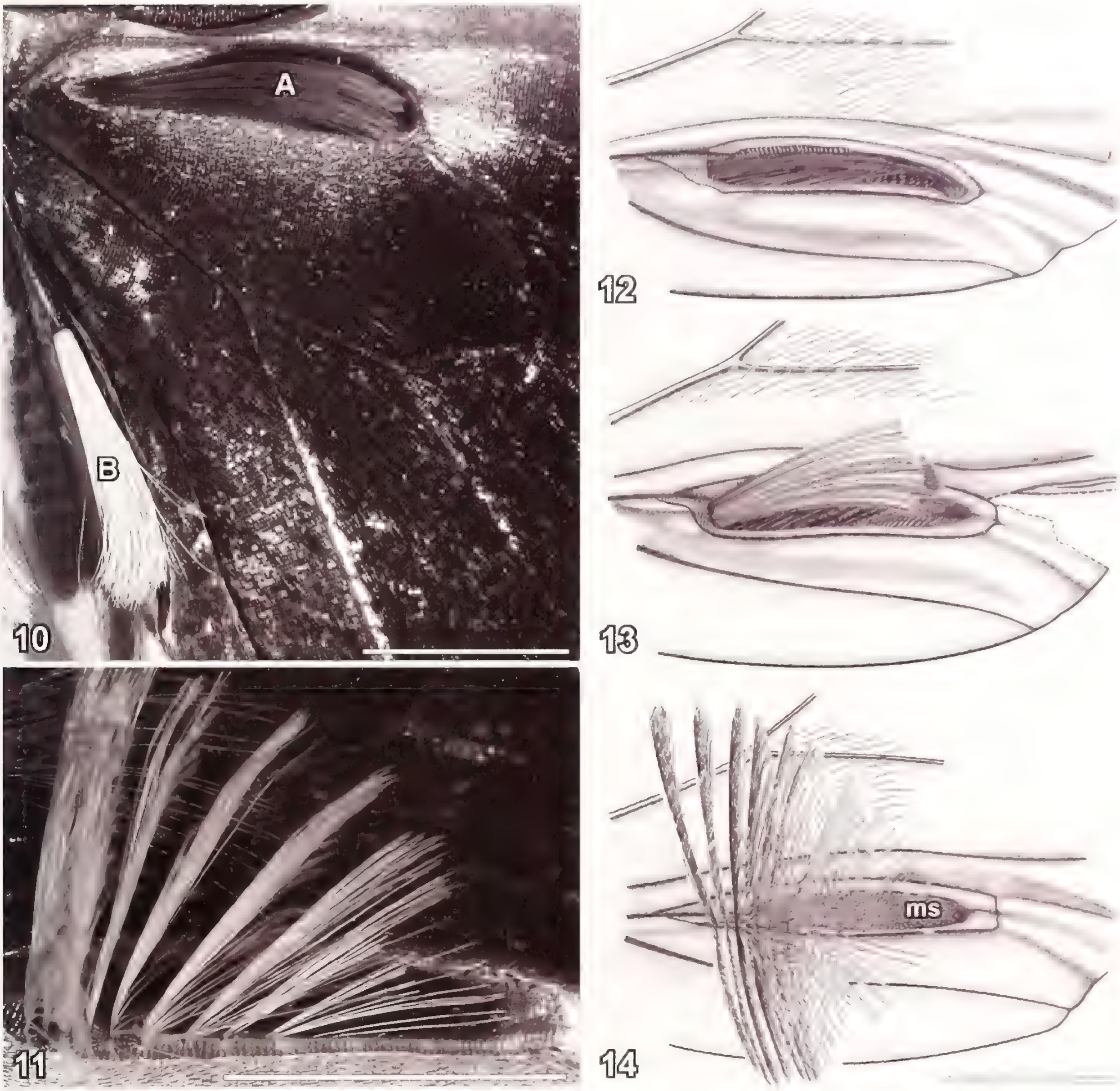
Currently, of the subgroups included by MILLER in the Biinae, only the evening browns and their relatives of the Old World tropics (Melanitini), together with the peculiar New World *Manataria*, appear to belong securely to the Satyrinae as currently conceived (ACKERY 1988; BROWER 2000; WAHLBERG et al. 2003). YOSHIMOTO (2003) has formally raised the Melanitini (to include *Manataria*) to tribal rank within the Satyrinae. Following DEVRIES et al. (1985), the Antirrheina are now widely accepted to as a subtribe of the Morphini (ACKERY 1988; HARVEY 1991; BROWER 2000). But what conclusions should be drawn with respect to *Bia*?

Appreciating the peculiarity of *Bia* is confounded by MILLER's description of the adult insect, which is inaccurate with respect to the labial palpi and forewing radial venation (the latter error has recently been repeated by YOSHIMOTO 2003), and incomplete most notably with respect to the androconial organs. In the following sections we first correct MILLER's (1968) account of the palpi and forewing venation. This is followed by observations on its wing patterns and an extensive account of the androconial organs. We then review recently published work on the early stages, hostplant relationships and molecular systematics, before offering a general discussion. Finally, we summarise a revised provisional classification for Satyrinae and Morphinae (Appendix I).

3. THE LABIAL PALP AND FOREWING RADIAL VENATION

Labial palp. MILLER's (1968: 33) account of the adult morphology of *Bia* is fundamentally incorrect on two points. First, regarding the labial palp, he states that "the third segment … is very long, over half the length of the second segment". Such an arrangement would be highly autapomorphic, but is simply not the case. As first shown by SCHATZ & RÖBER (1889: pl. 39), the third segment is much shorter, about one quarter the length of the second, as found in very many Nymphalidae.

Forewing radial venation. In contrast, as MILLER correctly appreciated, the forewing radial venation of *Bia* is highly autapomorphic, but his description ("forewing radial veins arise from a single branch") and illustration (MILLER 1968: 33, fig. 29) are inaccurate. The forewing radial system comprises two main branches, R_{1+2} and R_{3+4+5}, which arise in very close proximity at the anterior apex of the discal cell (Figs. 6, 7). After about 0.5 mm, R_{1+2} divides. R_1 then fuses with the subcostal vein for about 1 mm before separating again and finally running free to the costa (such an anastomosis occurs in many butterflies). R_2 runs free to the costa, but for the first 2 mm or so of its length it remains extremely close to R_{3+4+5}. After this parallel section, R_{3+4+5} gently diverges before separating, at about 5 mm from the apex of the discal cell, into R_3 and R_{4+5}; about 2 mm or so further on the latter separates into R_4 and R_5, with all the separate branches of R eventually running free to the costa. The real peculiarity of this system is the 'joint' origin (Fig. 7) of two branches of the radius as R_{1+2} and R_{3+4+5}, and their extremely close, parallel course that continues as R_2 and R_{3+4+5} (Fig. 6).

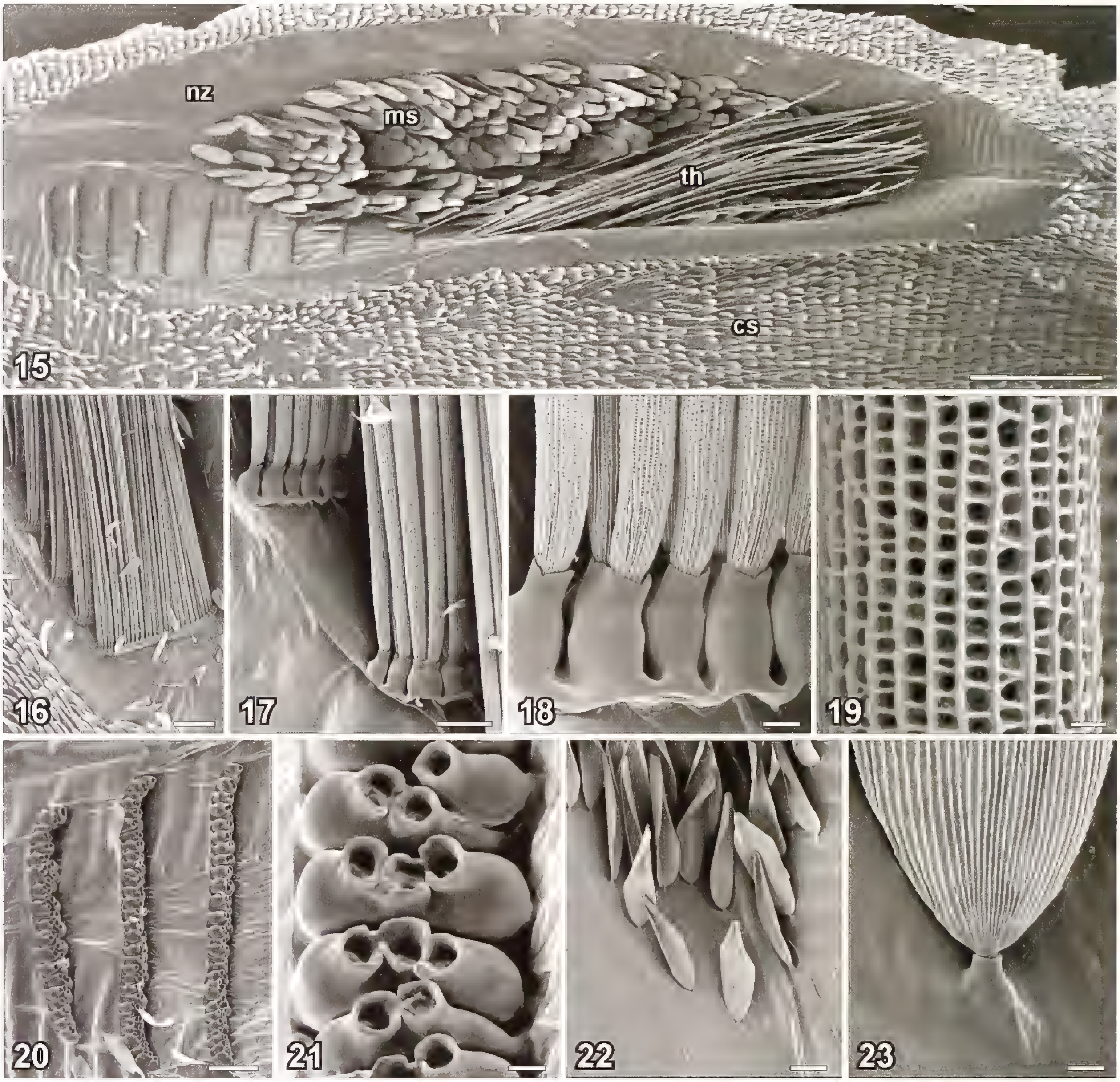


Figs 10–14: *Bia actorion* (L.) *sensu lato*. Hindwing androconial organs. **10** anterior (A) and posterior (B) alar organ; **11** posterior hair tuft fully erect; **12** pocket between 2A and 3A exposed with tuft closed (BMNH(E) #693030); **13** tuft partly erect revealing part of scale patch (BMNH(E) #693232); **14** tuft fully erect, patch of modified scales (ms) visible (BMNH(E) 693196). Scale bars: 10–14: 5 mm.

4. WING PATTERN

The underside pattern of *Bia* is very reduced compared with the nymphalid groundplan (NIJHOUT 1991: 24). Almost the entire area of both wings is covered by a ripple pattern (Figs. 3–5) (NIJHOUT 1991: 37), relieved only by marginal and submarginal bands on both wings, three or four specialised border ocelli and the parafocal elements on the forewings, and some very reduced ocelli and a few other markings on the hindwings, including the small but characteristic diagonal white stripe in cell Cu_{1a} (Figs. 3–5).

The forewing border ocelli, although small, are distinctive, occurring very close to the wing margin, with the two or three anterior ocelli (R_4 and R_5, and in some individuals, R_3) being reduced to white 'pupils' only (Figs. 3, 4). The posterior ocellus (in cell M_1), although better developed, is somewhat oblate, with the proximal side a little drawn out to form a blunt point. The parafocal elements of the forewing are not overwhelmed by the ripple pattern (cf. NIJHOUT 1991: 37), but form a distinctive line that deviates more or less markedly at the intervenous stripe in cell M_3. On the hindwing the border ocelli are reduced to vague spots, present only in

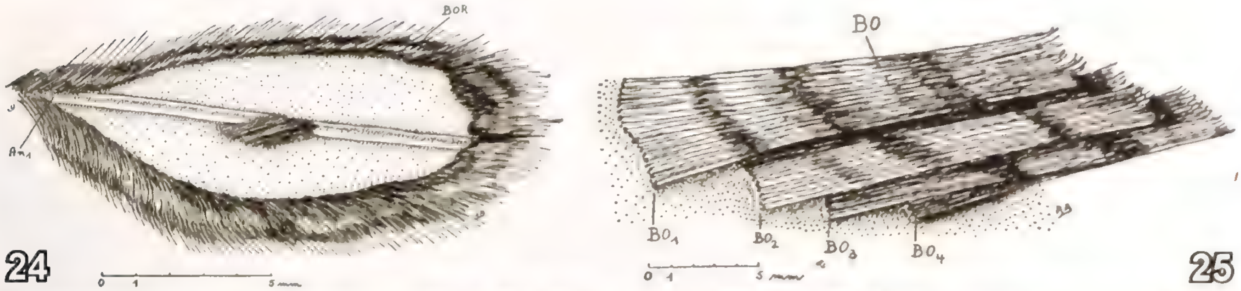


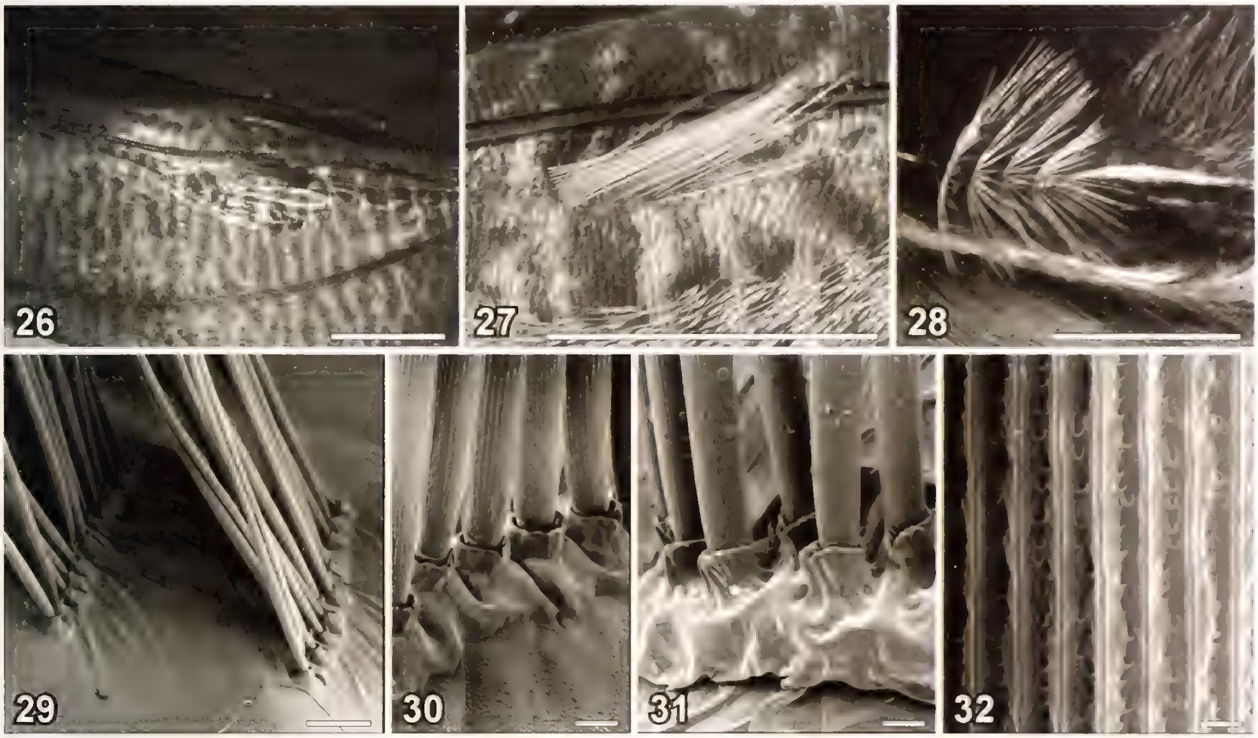
Figs 15–23: *Bia actorion* (L.) *sensu lato*. Scanning electron micrographs of hindwing posterior androconial organs. **15** entire organ with hairs from ten anterior tuft rows broken off to reveal a patch made of modified scales (ms) (22, 23), surrounding naked zone (nz), tuft hairs (th), and covering scales (cs) of wing area adjacent to vein 3A; **16** bases of a five rows of palisade-forming tuft hairs; **17**, **18** bases of a row showing conjoined sockets; **19** fine structure of hair; **20** part of patch with hairs lifted off to reveal sockets; **21** detail from sockets with hairs removed; **22**, **23** details of scales and sockets comprising patch (ms in 15). Scale bars: 15: 1 mm; 16: 200 µm; 17: 50 µm; 18: 10 µm; 19: 2 µm; 20: 100 µm; 21: 10 µm; 22: 100 µm; 23: 10 µm.

three adjacent anterior cells, R_1, R_5 and M_1, plus a diagonal whitish stripe in Cu_{1a} (which is also a specialised border ocellus – see Discussion). Although the three anterior hindwing ocelli occur in cells that, in terms of serial homology, correspond to the forewing cells that always have border ocelli, unlike the forewing, on the hindwing the ocelli are located far from the margin (Figs. 3, 4).

5. ANDROCONIAL SYSTEM

Alar androconial organs. According to MILLER (1968: 34), "there is a patch of mealy scales on the upper end of the cell along crossvein rs-m1, and a long hair tuft lies along 2A." As long ago and more accurately pointed out by MÜLLER (1877), the males of *Bia* possess a "tuft of long pale leather-brown hairs near the inner margin of the hind-wings, which can be erected or depressed at will, and when at rest, are enclosed in a long pocket, and also by a patch with long black silky hair





Figs 24, 25: *Caligo arisbe* Hübner, 1822. Hindwing posterior androconial organs (from BARTH 1953: figs 6, 7). Barth has called the structure 'apparatus assisting evaporation of the secretion'. An_1: analis of hindwing; dotted: naked area; BOR: ring of bristles; BO: bristles. [Note: obviously, the scale bar in 25 is incorrect.]

Figs 26–32: *Caligo eurilochus* (Cramer). Macrophotographs (26–28) and scanning electron micrographs (29–32) of hindwing posterior androconial organs. **26** hair tuft surrounded by a large shiny zone; **27**, **28** partly (27) and fully (28) erected hair tuft; **29–31** tuft rows showing conjoined sockets of palisade-forming tuft hairs; scanning electron micrographs: **32** fine structure of hair. Scale bars: 26–28: 5 mm; 29: 100 µm; 30, 31: 20 µm; 32: 2 µm.

near the anterior margin of the hind-wings. This latter patch is covered by a bare spot on the under side of the fore-wings, close to the inner margin." (cf. Figs. 1, 10).

Close examination of the hair tuft of the posterior alar organ (Figs. 11–21) reveals a peculiar arrangement of the hairs from which it is formed. The tuft comprises several rows of transversely inserted hairs, the length of the hairs, the distance between the rows, and the number per row all diminishing posteriorly (Figs. 11, 15; th), so that the entire tuft fits into a pocket formed between veins 2A and 3A. The whole organ, in its retracted state, is about 6–7 mm in length. When the hairs are erect, single lines become apparent, forming palisades (Figs. 11, 12, 14). The fine structure of these hairs (Fig. 19) is typical for many Lepidoptera androconia but their bases are peculiar in being conjoined (Figs. 18, 21). Underneath the hair tuft there is a large patch of modified scales (Figs. 14, 15; ms) that was overlooked by MÜLLER (1877). The scales are densely packed and partly upstanding, but do not show any peculiar features under SEM (Figs. 22, 23) or have sockets (Fig. 23) suggestive of glandular nature. Under a strong electron beam, these scales twist, something that happens to some scales but is relatively unusual. Adjacent to the posterior organ on the side abutting vein 3A is an extensive area of the wing with covering scales that are less dense and with scattered hairs (Fig. 15; cs), unlike the main areas of the wing.

In several specimens, the upperside forewing cell Cu_{1b} has a mane composed of hairs that are significantly longer and more densely packed than those found on the rest of the wing. This may represent another androconial organ, perhaps characteristic of one or more of the sibling species of which *Bia* may be composed, and is subject to further study.

MÜLLER (1877) found all kinds of "hair-tufts and felted patches" on the wings of male butterflies, including various Satyrinae and Morphinae. For *Caligo* he noted "Hind-wing of the male with a small tuft of hair near the inner margin, opposite to the middle of the abdomen." However, he apparently did not realize that the arrangement of the posterior hair tuft in *Bia* shares some peculiar features with *Caligo* (BARTH 1953; cf. figs. 24, 25), *Penetes* Doubleday, 1849, *Catoblepia* Stichel, 1902, *Opsiphanes* (ELTRINGHAM 1926; BARTH 1952), *Blepolenis* Röber, 1906, and *Caligopsis* Seydel, 1924, and some other brassolines. The most striking similarity is that the rows of tuft hairs arise from conjoined sockets (Figs. 24, 25, 27–32), a configuration currently unknown elsewhere in the butterflies. However, each row in these other genera comprises only a single line of scales (Fig. 29), not a double or triple line as in *Bia* (Figs. 17, 20, 21). Also, the number of rows of hairs (Figs. 27, 28) forming the posterior alar organ is always less, sometimes as few as 3 rather than 11–15 found in *Bia*. The major difference is the lack of a scale patch, but the surrounding zone (Figs. 24, 26) is comparable, normally much larger and conspicuous as a shiny, nacreous area (= "Reibefläche" of STICHEL 1909).

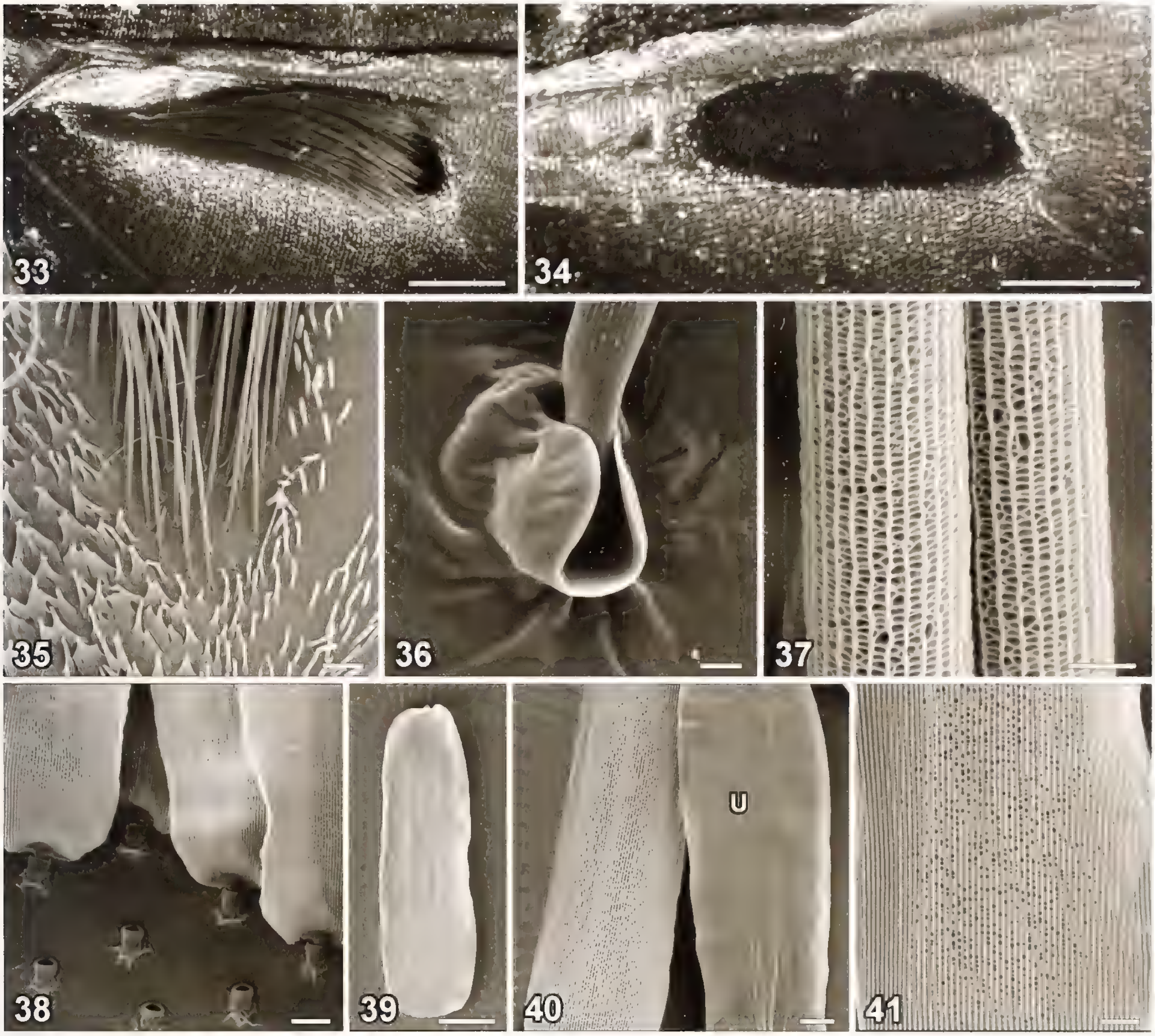
The anterior alar androconial organ of *Bia* consists in part of a pencil of hairs about 6–7 mm long (Fig. 33) inserted on the upperside close to the base of the hindwing discal cell (Fig. 10), and aligned approximately with the radial sector. It is evident that this pencil can be erected, as the hair sockets are modified to form an obvious 'click' mechanism (Fig. 36) comparable to that observed in the forewing alar organ of the morphine *Antirrhea* (Vane-Wright 1972b). These hairs do not otherwise exhibit special morphological peculiarities (Fig. 37), but when decumbent (Fig. 33) they virtually cover an extensive patch of modified scales (Fig. 34). This scale patch was not mentioned by MÜLLER (1877), but MILLER (1968: 34, fig. 29) referred to it (or the organ as a whole) as "a patch of mealy scales on the upper end of the cell." Probably a dual organ in the terminology of BOPPRÉ & VANE-WRIGHT (1989: 123), the hairpencil and its patch lie directly opposite a completely naked area on the underside of the forewing (MÜLLER 1877). A dual anterior alar organ of this type located in the hindwing discal cell is not typical for the Brassolini, but many members of the tribe have androconial organs of various sorts, including hairpencils located at various positions on the wings (cf. STICHEL 1909). *Caligo*, for example, has a conspicuous area of scales on the upper surface of the hindwing discal cell (Figs. 70–74) but, unlike *Bia*, this patch in *Caligo* is not associated with a hairpencil. *Eryphanis* Boisduval, 1870, has a patch and a hairpencil (ELTRINGHAM 1926), but the latter does not rest on the former.

Abdominal androconial organs. STICHEL (1909) mentions for many brassolines, including *Caligo, Penetes, Opsiphanes, Catoblepia,* and *Eryphanis*, "Reibewülste" or "drüsenartige Wülste" (rubbing or glandular bulges) that occur laterally on the male abdomina; no further characterisation is given. *Brassolis* Fabricius, 1807, *Dynastor* Doubleday, 1849, *Dasyophthalma* Westwood, 1851, *Narope* Doubleday, 1849, *Opoptera* Aurivillus, 1882, and *Selenophanes* Staudinger, 1887, lack them. These structures were not mentioned by MÜLLER (1877), but they have been described in considerable detail by BARTH (1952, 1953), and also by WASSERTHAL & WASSERTHAL (1977; as "scent pads"). Some of these structures are figured here for *Caligo eurilochus* (Cramer, 1775) (Figs. 63–69).

For the first time we describe lateral abdominal pads in *Bia* (Figs. 42, 44–46). Unfortunately, the condition of the specimens available to us is not suited for detailed study. However, in contrast to *Caligo*, the pads of *Bia* are located on the tergites (Figs. 42–46), not within the pleurae (Fig. 63). Moreover, in *Bia* the pads are comprised of three relatively simple scale types (Figs. 47–60), none of which matches the single highly specialised type (Figs. 64–69) of *Caligo*. The abdominal pads of *Caligo* can be protruded (WASSERTHAL & WASSERTHAL 1977). One set specimen of *Bia* in the collection of the BMNH shows the pads protruded, appearing as warty, shiny structures (Figs. 61–62). Another difference between *Caligo* and *Bia* concerns the resting position: in *Caligo*, when the butterfly is at rest, the pads are enclosed by the anal area of the hindwings, and thus must come automatically in contact with the posterior alar organs. In *Bia*, however, the posterior alar organ at rest is enfolded, and contact with abdominal pads would require a special behaviour. While *Caligo* exhibits dual androconial organs, those of *Bia* appear to be binate (BOPPRÉ & VANE-WRIGHT 1989). Although there are many differences in detail, the abdominal pads of *Bia* are grossly similar those found in Brassolini, and androconial organs of this general type are unknown from other taxa.

6. EARLY STAGES AND HOSTPLANT RELATIONSHIPS

Until the publication by FREITAS et al. (2002), the life cycle of *Bia* was undescribed. Here we summarise their results with reference to features of the early stages considered likely to be of significance for higher classification.

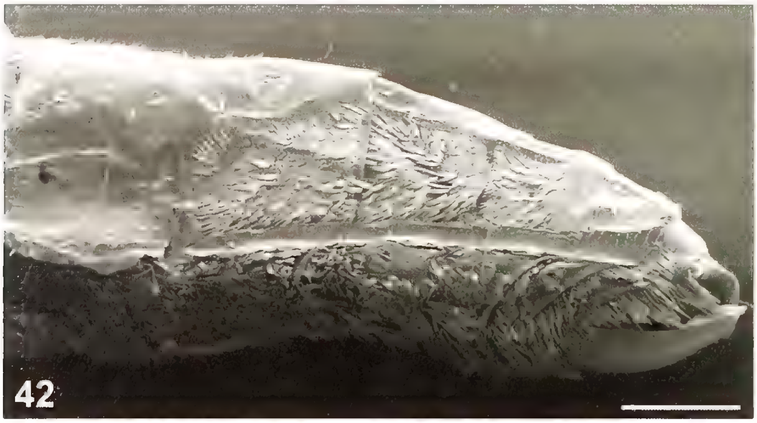


Figs 33–41: *Bia actorion* (L.) *sensu lato*. Macrophotographs (33, 34) and scanning electron micrographs (35–41) of hindwing anterior androconial organs. **33** hair tuft in resting position, obscuring **34** patch with modified scales; scanning electron micrographs: **35**, **36** hair bases exhibiting 'click' mechanism; **37** fine structure of hair; **38–41** patch scale bases and scale fine structure are unexceptional but the scale undersides are not perforated (40, U). Scale bars: 33, 34: 2 mm; 35: 100 µm; 36, 37: 5 µm; 38: 20 µm; 39: 50 µm; 40: 20 µm; 41: 10 µm.

Egg. Spherical, with 25–30 longitudinal ribs and as many as 50 transverse ridges (FREITAS et al. 2002: 120, fig. 1a). The eggs are thus comparable to those of Brassolini, which have 30–60 transverse ridges (e.g. *Narope*: CASAGRANDE 2002: figs. 1,2), and are unlike those of Satyrinae, which never have as many (FREITAS 1999).

First instar larva. The head capsule lacks scoli but has numerous long, branched or plumose setae (FREITAS et al. 2002: figs. 1b,c). A very similar condition can be seen in some Brassolini (e.g. *Narope*: CASAGRANDE 2002: fig. 4). FREITAS et al. (2002: 119) note that the newly hatched larvae are active, moving around the hostplant unlike "the sluggish behaviour of typical satyrines".

Later instar larvae. Later instars have three pairs of scoli on the head capsule (FREITAS *et al.* 2002: 121, figs 1i,j,k), typical of most Brassolini other than *Brassolis* (cf. DEVRIES 1987: fig. 32 E, 1–8; CASAGRANDE 2002: fig. 3e). According to FREITAS et al. (2002: 121), Satyrinae only have one pair of such scoli; however, while this is generally the case, arguably *Elymnias* Hübner, 1818, also has three pairs (IGARASHI & FUKUDA 1997: 85–89). The form of the head scoli in *Bia* is, however, highly autapomorphic, especially the dorsal pair (FREITAS et al. 2002: fig. 1k). The bifid caudal projec-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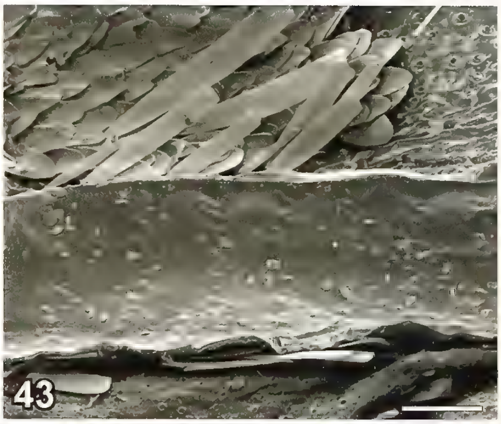
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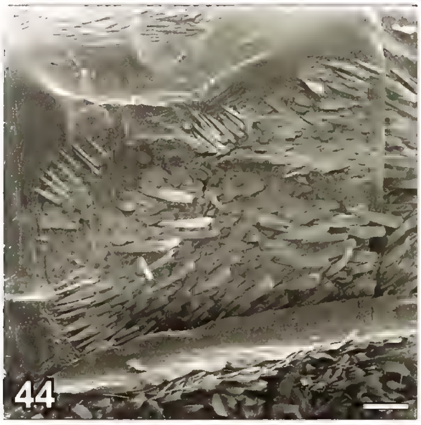
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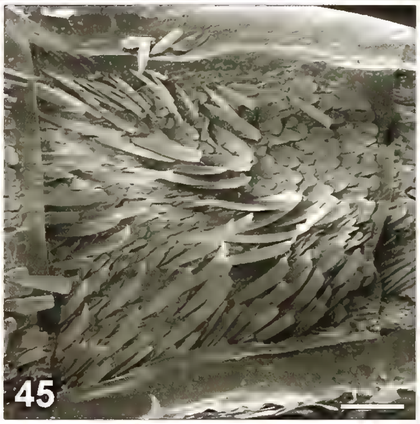
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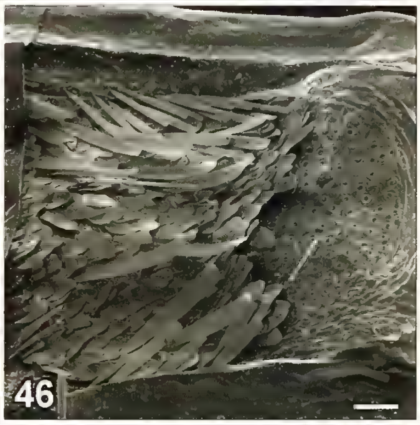
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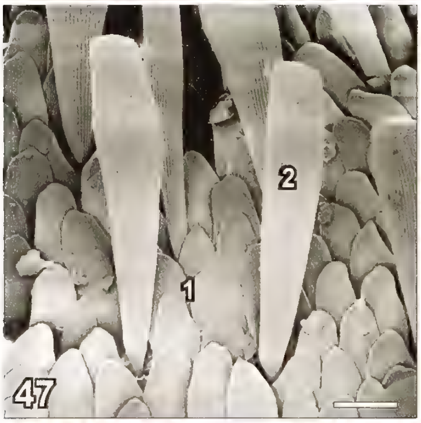
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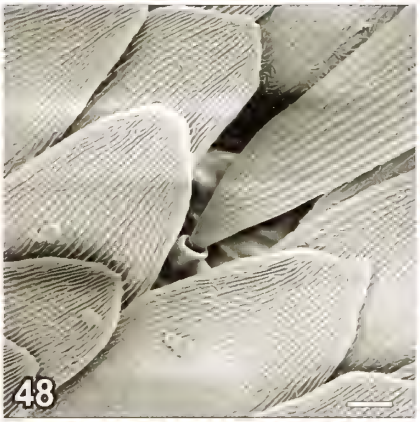
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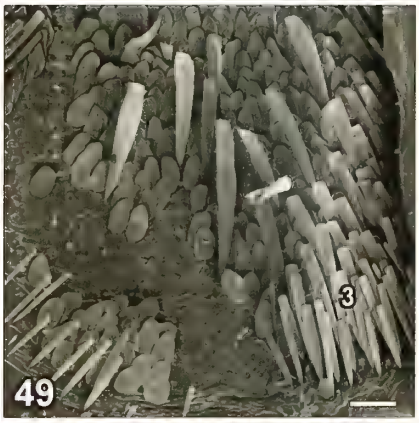
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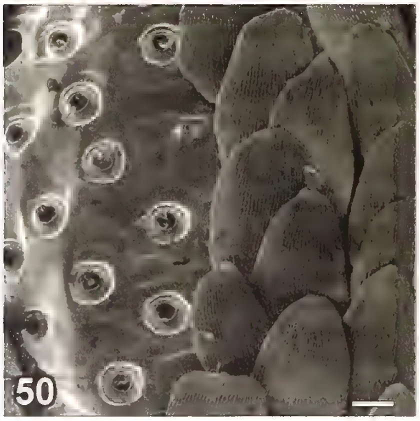
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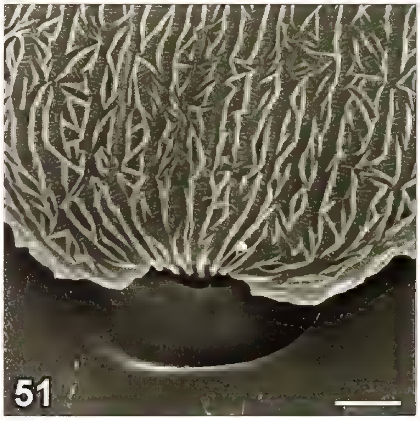
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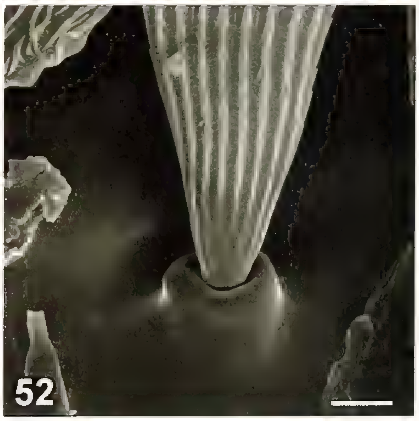
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tions (Freitas et al. 2002: figs. 1b,f,g,h,i) are like those seen in many Brassolini (e.g. *Caligo*: Casagrande 1979), and are thus grossly similar to all members of the Satyrine clade as conceived by Freitas & Brown (2004), including Amathusiini, Calinaginae and Apaturinae. The numerous secondary body setae give a "hairy" appearance, as in many Brassolini (e.g. *Caligo*: Casagrande & Mielke 2000a: fig. 3) and Amathusiini (Igarashi & Fukuda 1997).

Pupa. Squat and sculptured (Freitas et al. 2002: fig. 1 l,m), and thus quite similar to e.g. *Opsiphanes* (DeVries 1987: fig. 32B) and *Dasyopthalma* (Casagrande & Mielke 2000b: figs 6–8; 2003: figs. 4–6).

Hostplants. *Astrocaryum* G.Mey, 1818, and *Geonoma* Willd., 1805 (Arecaceae) (Freitas et al. 2002). Arecaceae are recorded as foodplants of species of the brassoline genera *Brassolis, Opsiphanes, Catoblepia* and *Dasyophthalma*, and are also utilised by some species of Morphini, Amathusiini and Satyrinae (Ackery 1988). Among the Brassolini, *Geonoma* is recorded as the host of *Dasyophthalma* species (Cassangrande & Mielke 2000b, 2003), both *Geonoma* and *Astrocaryum* are recorded as hosts for *Opsiphanes* (Penz et al. 2000), and *Astrocaryum* as a host for *Brassolis* (Ackery 1988).

7. MOLECULAR EVIDENCE

Brower (2000) carried out a cladistic analysis of 103 species of Nymphalidae based on sequence data obtained from a 378 base-pair region of the *wingless* gene. In addition to *Bia*, his sample included species representing 6 genera conventionally included in the Morphinae *sensu lato* (*Morpho, Caerois, Antirrhea, Amathusia, Caligo* and *Opsiphanes*), and 13 genera included in the Satyrinae (*Haetera* Fabricius, 1807, *Melanitis, Lethe* Hübner, 1819, *Mycalesis* Hübner, 1818, *Tisiphone* Hübner, 1819, *Megisto* Hübner, 1819, *Oressinoma* Westwood, 1852, *Taygetis* Hübner, 1819, *Cercyonis* Scudder, 1875 , *Corades* Doubleday, 1848, *Lymanopoda* Westwood, 1851, *Pedaliodes* Butler, 1867, and *Steroma* Westwood, 1851). In his preferred solution (a most parsimonious cladogram produced using the successive approximations weighting option in PAUP 3.1: Swofford 1991), all 20 of these genera, including *Bia*, formed a monophyletic group. This was divided into two subclades, one including the 13 genera conventionally included in the Satyrinae plus *Amathusia*. The remaining five conventional morphines, plus *Bia*, formed the other group. Within this latter clade, *Bia* grouped as sister to *Caligo*, with *Opsiphanes* as sister to these two, with these three forming the sister group to (*Morpho* (*Antirrhea* + *Caerois*)).

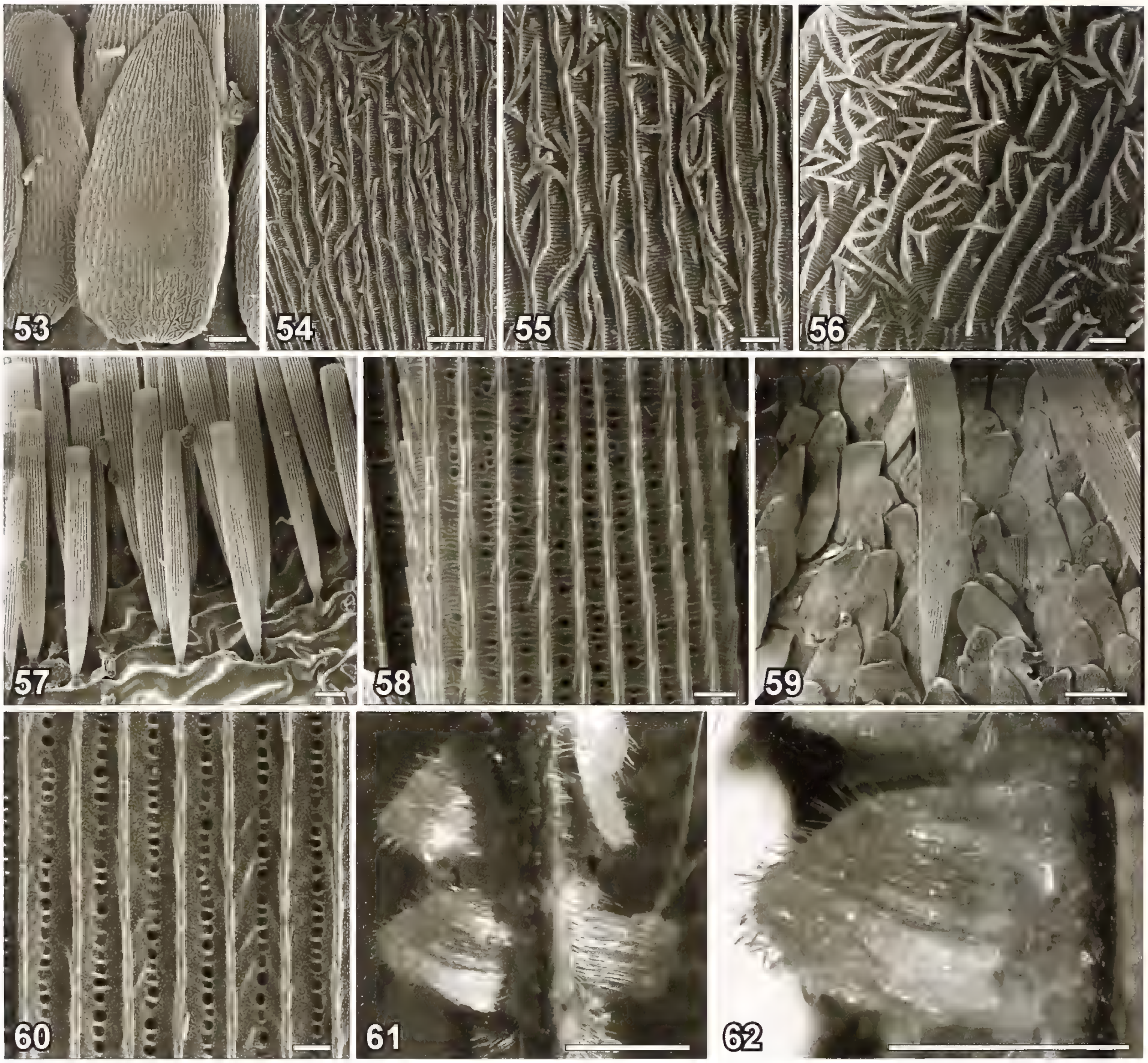
Wahlberg et al. (2003) presented results from a cladistic analysis of 54 Nymphalidae, based on sequence data for one mitochondrial gene (COI, 1450 bp) and two nuclear gene sequences (EF-1α, 1064 bp; and *wingless*, 412–415 bp). His species sample represented three conventional morphine and nine conventional satyrine genera, including *Manataria* but not *Bia*. Although all of these genera grouped within a single major subclade, this grouping also encompassed both of their exemplar Charaxinae, and the enigmatic *Calinaga* Moore, 1857 (Calinaginae). This last genus (not available to Brower) grouped as sister to the two Charaxinae, and in some analyses these three together appeared as the sister group to (*Caligo* + *Morpho*). The remainder of the clade formed a paraphyletic assemblage of the nine conventional Satyrinae including *Melanitis* and *Manataria*, together with *Stichophthalma* C. & R. Felder, 1862 (Amathusiini). *Manataria* appeared as sister to *Melanitis*, and did not group with any of the Satyrini or Elymniini included in the analysis. This offers support for the inclusion of *Manataria* within the Melanitini as dealt with by Yoshimoto (2003), and not in the lethines (Elymniini) as vaguely speculated by Miller (1968), or in the Euptychiina (Satyrini) as suggested by Forster (1964).

8. DISCUSSION

Miller (1968: 33) made two errors in his account of *Bia*. First, he stated that the third segment of the labial palpus was abnormally long, exceeding half the length of the second. As revealed even by his own diagram (Miller 1968: fig. 30), this is simply inaccurate. The gross morphology of the *Bia* palp is commonplace and unremarkable, being directly comparable to brassolines such as *Aponarope* Casagrande, 1982 (Casagrande 2002: fig. 103), and many other nymphalids.

Miller's description of the forewing venation was also wrong: two branches of the radius (R_{1+2} and R_{3+4+5}) arise from the cell, not one. Miller (1968: fig. 29) was misled because the anterior of the two branches arising from the cell, R_{1+2} and its continuation as the basal part of free R_2, lies parallel to R_{3+4+5}, the two sections initially running very close together (Fig. 7). He was nonetheless correct to regard the venation as very peculiar.

Figs 42–52: *Bia actorion* (L.) *sensu lato*. Scanning electron micrographs of abdominal androconial organs. **42** lateral view of abdomen from segment 3 to apex, showing position of lateral pads on tergites of segments; **43** channel-like strukture formed by pleurae; **44–46** pads on segment 4–6; **47** short (type 1) and long (type 2) androconial scales clothe all three pads; **48** detail of 47; **49** small marginal scales (type 3); **50, 51** scale bases of type 1; **52** scale base of type 2. Scale bars: 42: 1 mm; 43: 100 µm; 44, 45: 200 µm; 46: 100 µm; 47: 50 µm; 48: 10 µm; 49: 100 µm; 50: 20 µm; 51, 52: 5 µm.



Figs 53–62: *Bia actorion* (L.) *sensu lato*. Scanning electron micrographs of abdominal androconial organs. **53–56** details of scale type 1; **57**, **58** details of scale type 3; **59**, **60** details of scale type 2; macrophotographs: **61**, **62** dorsal views of abdomen of unique museum specimen in which the pads are exerted. Scale bars: 53: 10 µm; 54: 5 µm; 55, 56: 2 µm; 57: 20 µm; 58: 2 µm; 59: 50 µm; 60: 2 µm; 61–62: 1 mm.

Although the forewing radial vein configuration of *Bia* is unique among the butterflies, it can be compared in some ways with the Brassolini: Naropina (genera *Narope* and *Aponarope*), in which three branches of the radius arise in close proximity from the discal cell, with either a single anastomosis of $Sc+R_1$ (CASAGRANDE 1989: fig. 5), or a double anastomosis giving a short section $Sc+R_{1+2}$, with $Sc+R_1$ and R_2 eventually running separately to the costa (STICHEL 1904: pl. 1, fig. 5; CASAGRANDE 1989; 1996: fig. 29). The venation of *Bia* is also comparable to that of certain amathusiines, such as *Discophora*, in which the forewing radial system similarly arises from the discal cell as two branches that run closely parallel. However, the two branches in *Discophora* are R_1 and Rs (not R_{1+2} and R_{3+4+5}). In this genus R_1 forms a long anastomosis with Sc before separating, then forms an anastomosis with R_2 before they separate and run free to the costa (BASCOMBE et al. 1999: fig. 9.38).

But even if MILLER had been right regarding the palp, two such autapomorphies would have told us little about relationships. The odd venation even when correctly described, simply underscores the generic distinctness of this peculiar nymphalid. This would also be true with respect to the absence of tibial spurs, another unusual feature of *Bia* observed by MILLER (1968: 33, fig. 31). In this context it may be significant that *Narope* also lacks tibial spurs, whereas its close relative *Aponarope* does not (CASAGRANDE 2002: figs. 30a,b, 103a,b). However, before drawing any detailed conclusions about the relationships of *Bia*, we first discuss a series of wider questions regarding its higher classification.

Does *Bia* belong to the satyrine clade? In nymphalid butterflies other than *Bia*, ripple patterns (NIJHOUT 1991) are found in the Nymphalina (e.g. *Nymphalis* Kluk, 1802, *Aglais* Dalman, 1816, *Polygonia* Hübner, 1819), Satyrinae (many species, including *Melanitis*, *Elymnias* and *Ypthima* Hübner, 1818), Morphinae (all Brassolini; Morphini: Antirrheina; and a few Amathusiini, including *Thauria* Moore, 1894, and *Discophora*), and certain Charaxinae (including *Palla* Hübner, 1819, and *Anaea* Hübner, 1819). Thus the capacity to produce underside ripple patterning appears to be a characteristic (with the exception of the Nymphalina) of the satyrine clade *sensu* WAHLBERG et al. (2003) as based on molecular evidence, or the satyroid clade *sensu* FREITAS (1999) other than the supposedly basal Apaturinae (FREITAS & BROWN 2004) as based on early stage characters. Other than in the Nymphalina, ripple patterns are unknown elsewhere in the Nymphalidae, including the very small subfamily Calinaginae (considered internal to the satyrine clade by BROWER 2000, WAHLBERG et al. 2003, and FREITAS & BROWN 2004), and the Apaturinae (not included in the satyrine clade by BROWER 2000 or WAHLBERG et al. 2003). Based on many characters including features of the thorax, EHRLICH (1958) placed *Bia* in the Nymphalidae: Satyrinae. With the recent addition of molecular and early stage data, there is now little doubt that *Bia* belongs to the satyrine clade *sensu* WAHLBERG et al. (2003), and its ripple pattern (Figs. 3–5) is further evidence from adult morphology consistent with this conclusion.

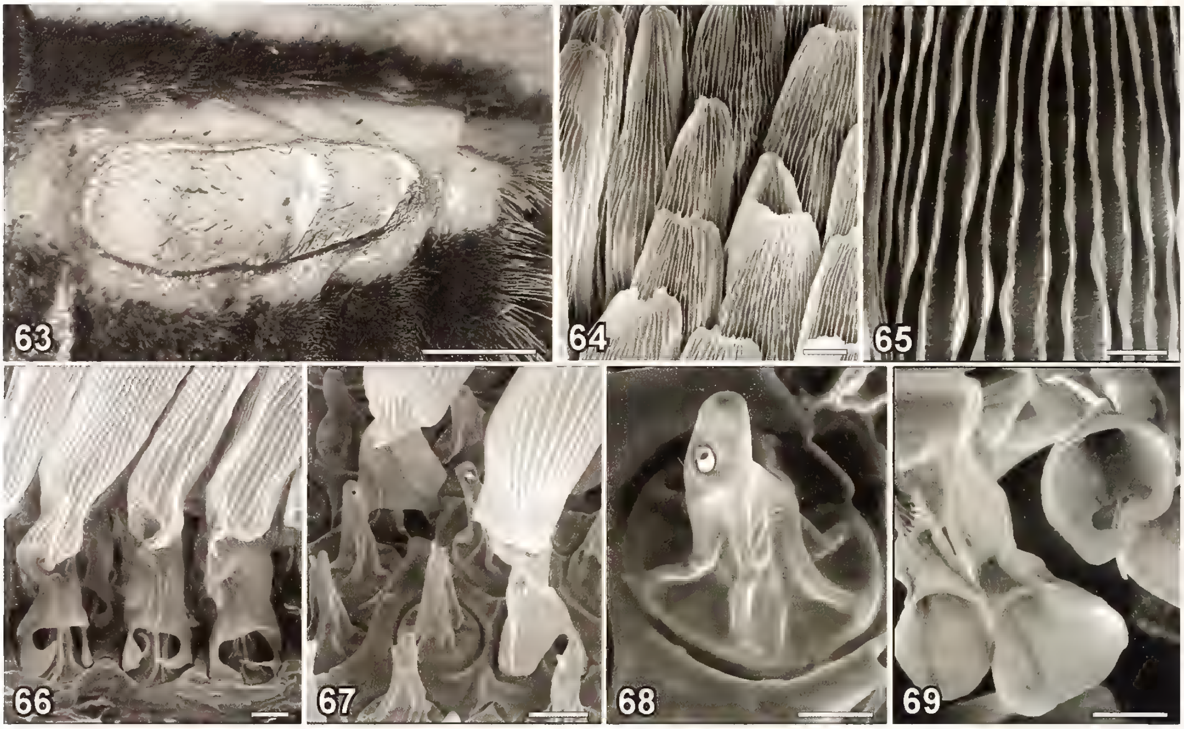
Why isn't *Bia* a satyrine? As reviewed above, most authors have included *Bia* within the Satyrinae, including EHRLICH (1958), MILLER (1968), and HARVEY (1991). The emergent view, however, is that *Bia* belongs to the Morphinae: Brassolini (CLARK 1947, 1948; DEVRIES et al. 1985; BROWER 2000; FREITAS et al. 2002; VANE-WRIGHT 2003; YOSHIMOTO 2003). The question then naturally arises, what are the distinguishing features of the Satyrinae, and does *Bia* exhibit them or not?

Unfortunately, from a morphological perspective, no uniquely diagnostic features for the Satyrinae have been recognised (DEVRIES et al. 1985; HARVEY 1991; ACKERY et al. 1999). Traditional but non-unique characters include the closed hindwing discal cell, feeding on monocots, and the fleshy, bifid larval tail (MILLER 1968; ACKERY et al. 1999). Although *Bia* has all of these features, none is diagnostic for Satyrinae with respect to Morphinae. EHRLICH (1958) listed a number of characters for all subfamilies of the Nymphalidae that he recognised. For the Morphinae and Satyrinae the only clear separation he gave was another traditional character, the inflated forewing veins Sc, Cu and 2A never clearly seen in the Morphinae, but present in many Satyrinae. In this respect *Bia* is a typical satyrine and unlike the morphines. However, the expression of this character varies widely. For example, it is virtually unexpressed in Satyrinae: Melanitini, while only vein Sc is inflated in Satyrinae: Ragadiini. Moreover, inflated forewing veins occur elsewhere in the Nymphalidae, well outside the satyrine clade (EHRLICH 1958; ACKERY et al. 1999).

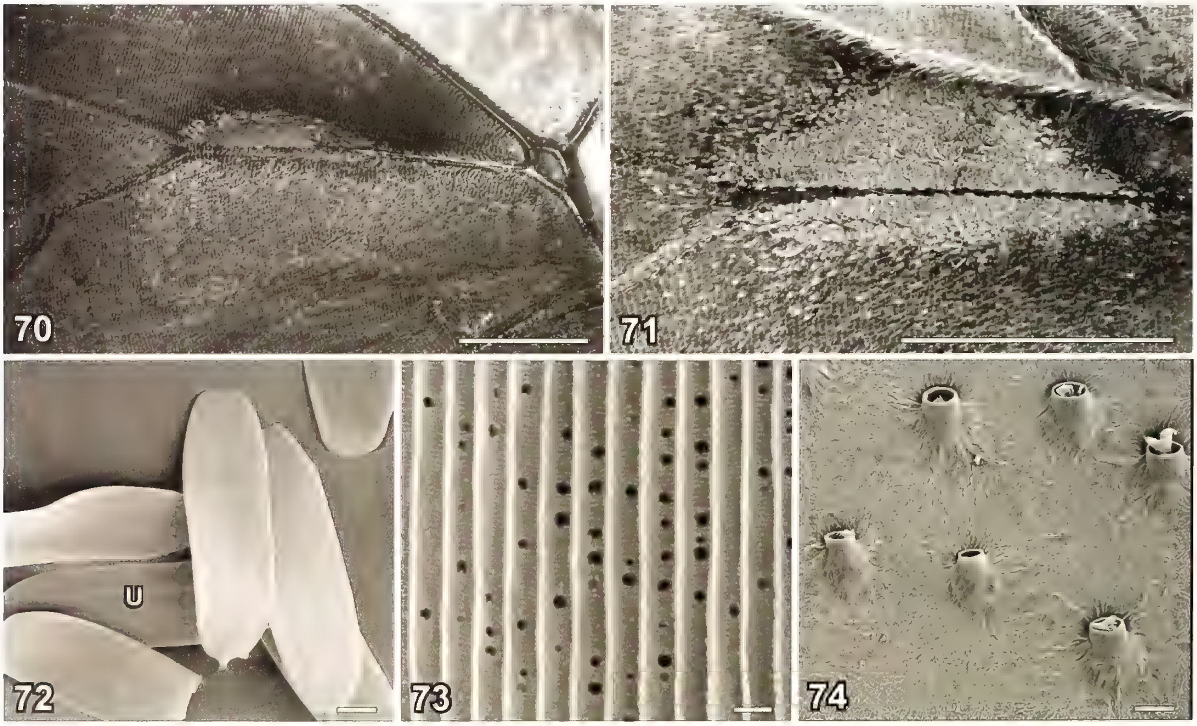
Why don't the Brassolini belong to the Satyrinae? Even if *Bia* were most closely related to the Brassolini, we must also consider the possibility that the Brassolini are simply nested, to the exclusion of the Morphini and Amathusiini, within the Satyrinae, as proposed by MILLER (1968). DEVRIES et al. (1985) re-affirmed EHRLICH's (1958) position by including the Brassolini and Amathusiini within the Morphinae, doing so primarily on the basis of three putative larval characters. However, DeVries later retained the Morphinae and Brassolinae as separate subfamilies, and commented that the latter were "closely related to the Satyrinae" (DEVRIES 1987: 245). HARVEY (1991), partly due to an error in interpreting ACKERY (1988) (see ACKERY et al. 1999), also kept the Brassolinae as a separate subfamily. Given all this uncertainty, and the fact that the larval characters introduced by DEVRIES et al. (1985) remain unverified for many relevant taxa, we must question whether or not it is correct to link the brassolines with the morphines, and whether or not they can legitimately be excluded from membership of the Satyrinae, either alone, or together with the Morphini.

Do the Brassolini belong to the Morphinae? In the molecular investigations of both BROWER (2000) and WAHLBERG et al. (2003), their exemplar Brassolini grouped exclusively with their exemplar Morphini, while the two Amathusiini (*Amathusia* in BROWER, *Stichophthalma* in WAHLBERG et al.) appeared elsewhere, either within a monophyletic Satyrinae (BROWER 2000: fig. 4), or as part of a paraphyletic assemblage made up of Satyrinae, Morphinae, Charaxinae and Calinaginae (WAHLBERG et al. 2003: fig. 4). This is consistent with the conclusion of EHRLICH (1958) that the Satyrinae and Morphinae *sensu lato* are closely related, as also suggested by KUZNETZOV & STEKOLNIKOV (2001), who linked the Morphinae *sensu* EHRLICH (1958) with the Satyrinae as a monophyletic family. The conclusions of FREITAS & BROWN (2004: fig. 5) also suggest that the Brassolini are more closely related to the Morphini (and the Amathusiini) than they are to the Satyrinae.

SCOTT (1985) considered that the larval "fuzzy head" characterised the Morphinae *sensu* EHRLICH (1958) as a



Figs 63–69: *Caligo eurilochus* (Cramer). Macrophotograph (63) and scanning electron micrographs (64–69) of abdominal androconial organs. **63** lateral view of abdominal segments 4-6 showing pad, located in the pleural area between the tergites and sternites; scanning electron micrographs: **64–69** scales making up pad; they exhibit unusual scale structure (65), and, in particular, highly specialised sockets (66–68); note tube leading from interior and funnel-like base that fits over the specialised sockets (69). Scale bars: 63: 2 mm; 64: 20 µm; 65: 5 µm; 66, 67: 20 µm; 68: 10 µm; 69: 20 µm.



Figs 70–74: *Caligo eurilochus brasiliensis* (Cramer). Macrophotographs (70, 71) and scanning electron micrographs (72–74) of hindwing anterior androconial organs. **70** patch immediately anterior to vein Rs (note also very small precostal cell); **71** detail of patch; scanning electron micrographs: **72** scales comprising patch (U: underside); **73** detail of scale surface; **74** scale sockets. Scale bars: 70–71: 5 mm; 72: 50 µm; 73: 2 µm; 74: 20 µm.

monophyletic group. If so, this raises doubts about inclusion of the Amathusiini within the Satyrinae. Certainly the larvae of various Amathusiini do have "fuzzy" heads (e.g. Igarashi & Fukuda 1997: pls. 126–133), comparable to Brassolini and Morphini. However, it is evident that the head capsule of *Melanitis*, for example, is also quite "fuzzy", and more work is needed on this character. Another character linking the Amathusiini to the Brassolini is the presumed repugnatorial neck gland of the larvae (Eliot, *in* Corbet & Pendlebury 1992: 137). Our conclusion is that, despite the weakness of the present evidence, we should maintain the Morphinae *sensu* Ehrlich (1958), to include Morphini, Amathusiini and Brassolini.

Is *Bia* a brassoline?

In Brower's (2000) analysis, and in some of the analyses of Freitas & Brown (2004), *Bia* groups with the Brassolini to form a monophyletic group, either with just the Morphini (Brower 2000; Freitas & Brown 2004: fig.1) or with the Morphini + Amathusiinae in addition (Freitas & Brown 2004: fig. 3). So the Brassolini do not appear to belong to the Satyrinae *sensu stricto*. Given the evidence from early stages reported by Freitas et al. (2002) that seem so suggestive that *Bia* is a brassoline (summarised in section 7 above), it is perhaps surprising that Freitas & Brown (2004: fig. 5) placed *Bia* as a monobasic subfamily separate from both Morphinae and Brassolinae. Apparently they did so because *Bia* behaved ambiguously in their analyses: "it appeared in three different positions in the trees" (Freitas & Brown 2004: 372). Can any strong support or challenge to the hypothesis that *Bia* is a brassoline be drawn from our re-examination of adult morphology?

Ackery et al. (1999) stated that the "Brassolini … currently lack convincing autapomorphies". Although Miller's (1968) arguments for including the Brassolini within the Satyrinae were unconvincing, he did identify one relatively distinctive character for the group apparently overlooked by Ackery et al. – the basal separation of the hindwing veins Sc and R_1 to produce a distinct precostal cell (Stichel 1909). Miller correctly pointed out that this feature recurs in a few groups included in the Satyrinae (e.g. *Elymnias*: Schatz & Röber 1889: pl. 39), and essentially the same character is found in some other butterflies, including many Papilionidae (Smith & Vane-Wright 2001), various Charaxinae (Schatz & Röber 1888: pls. 28, 29), *Parthenos* Hübner, 1819 (Limenitidinae: Schatz & Röber 1887: pl. 25), various Danaini (Ackery & Vane-Wright 1984), and even *Morpho* itself (Schatz & Röber 1885: pl. 1, fig. 1). Thus, although characteristic of all Brassolini, the precostal cell is not uniquely diagnostic for the group.

Within the Brassolini, as demonstrated by Stichel (1904, 1909), the precostal cell varies significantly in size and form. In some genera (e.g. *Opoptera*) it is very large (Stichel 1904: pl. 2, fig. 1), and most brassolines approach this condition. In *Eryphanis, Caligopsis* and *Caligo*, however, the precostal cell is much smaller, with a narrow, ovoid 'lumen' (Stichel 1904: pl. 2, figs. 4, 5), unlike the widely open 'parallelogram' seen in other genera. *Bia* has a slight basal separation of these veins, as correctly observed over 150 years ago by Westwood (1850), but this can only be appreciated readily by examination of a cleared wing preparation or use of SEM. The form this takes in *Bia* (Figs. 8, 9) is like a miniaturised *Eryphanis* or *Caligo* (Fig. 70). However, given the homoplasious distribution of this character as noted above, to include *Bia* within the Brassolini on this basis would be unconvincing.

The configuration of the forewing ocelli of *Bia* closely approximates that seen in several brassoline genera, notably *Opoptera*, *Catoblepia*, and many species of *Opsiphanes*. This is also true for the curvilinear path of the parafocal elements that occurs in some of the species belonging to these genera, including the deviation in cell M_3. Overall, this gives a reminiscent 'Gestalt' to both the upperside and underside pattern of the forewing apex of *Bia* and these three genera. On the hindwing underside the position of the ocellar marking in cell R_1 also corresponds closely to that occupied by the large and fully-developed border ocellus in underside cell R_1 of the same genera. The suggestion of a border ocellus in hindwing cell R_5 is unusual in most brassolines, while an ocellus in M_1 is only seen in a few genera, notably *Brassolis* and *Dasyophthalma*. However, in many species of *Narope* small border ocelli similar to those of *Bia* occur in all hindwing underside cells R_1–Cu_{1b} (e.g. Casagrande 2002: figs. 29, 95). Most Brassolini have an extremely well developed border ocellus in hindwing underside cell Cu_{1a}, reaching its maximum development both in size and basal displacement to give the huge eyespot characteristic of the owl butterflies (*Caligo*). Of this there is no obvious trace in *Bia*, unless we interpret the curious diagonal white stripe that occurs in cell Cu_{1a} adjacent to the tail-like extension formed around Cu_{1b} (also unique to this genus: the tail of *Opoptera* is formed around M_3) as a modified remnant of the ocellar pupil. This appears to be confirmed by the very similar underside white stripe that occurs in cell Cu_{1a} of some species of *Narope*, such as *N. cyllastros* Doubleday, 1849, and *N. cyllene* Felder, 1859 (Casagrande 2002: figs. 28, 29, 34, 35; cf. fig. 50).

Male genitalia are widely used in insect systematics, but these highly plastic structures are often difficult to interpret for higher taxonomy (Smith & Vane-Wright 2001). Most members of the satyrine clade have relatively simple male genitalia, and this is true for *Bia*

(HAYWARD 1958, 1964). Indeed, the genitalia of *Bia* are quite similar to *Narope*, except that the ganthos is directed ventrally (as in Brassolina), unlike the upswept structure found in Naropina (CASAGRANDE 1996: figs. 10–12, 31, 32).

As with the precostal cell, the wing patterns of *Bia* and perhaps even the male genitalia are suggestive of a relationship with the Brassolini, but are not wholly convincing. In contrast, several features of the androconial organs provide what we consider to be strong evidence for such a relationship. Notably, hair-tufts arranged in palisades with conjoined sockets and abdominal pads occur in many Brassolini, and in *Bia*, but not in the Satyrinae.

9. CONCLUSIONS

Evidence from all life stages, including several adult characters described here, and DNA sequence data, supports the view that *Bia* is a member of the morphine tribe Brassolini. Even though *Bia* is very small for a brassoline (forewing length 25–32 mm) and highly autapomorphic, it may ultimately prove to be internal to the tribe as a whole, and not sister to the rest of the group as suggested by one of the analyses made by FREITAS & BROWN (2004: fig. 2).

Until recently there has been no accepted subtribal classification for the Brassolini. However, CASAGRANDE (1996, 2002) has separated the Naropina Stichel (to include only *Narope* and *Aponarope*) from all of the remaining genera, which she included in the Brassolina. In addition to its marked autapomorphic features (e.g. forewing radial venation, inflated forewing veins, minute hindwing precostal cell, basally fused dorsal horns of larval head), *Bia* shares putative synapomorphies with both the Naropina (e.g. loss of tibial spurs; unique form of hindwing underside border ocellus in cell Cu_{1a}; possibly the plumose hairs on larval head) and the Brassolina (e.g. tufted alar organs composed of palisade rows and abdominal pads, as found in *Caligo* and several other genera). In the circumstances, we propose, pending more extensive analysis, to place *Bia* in the Biina Herrich-Schäffer, 1864, as a third subtribe of the Brassolini Boisduval, 1836 (see Appendix I). However, it seems quite possible that the Biina will ultimately be subsumed within the Brassolina, or subsume the Naropina.

BOPPRÉ (1984) commented that “androconial organs are … analogous structures, convergently evolved many times … [and] of limited taxonomic value, although they certainly provide good characters in some groups”. Despite this rather cautious view, our experience over the intervening 20 years suggests that detailed investigations of androconial organ morphology (e.g. BOPPRÉ & VANE-WRIGHT 1989), even though loss and independent gain of these organs are indeed frequent evolutionary phenomena, can provide extremely valuable insights into systematic relationships (e.g. VANE-WRIGHT et al. 2002; cf. HALL & HARVEY 2002). This can also be true of androconial chemistry, as in the Danaini (VANE-WRIGHT & BOPPRÉ 1993; SCHULZ et al. 1993), although SCHULZ et al. (2004) found relatively little evidence for phylogenetic relationships from their analyses of Ithomiini pheromones. In the case of the two Neotropical tribes of Morphinae, abdominal coremata are diagnostic for the Morphini, while palisade alar organs and abdominal pads appear to be autapomorphic for Brassolini (including *Bia*), even though they are not expressed by all members of the group.

We conclude that a combined morphological and chemical investigation into the scent organs of *Bia* and other Brassolini would be a most interesting and potentially instructive challenge. Such a study would be in the best tradition of Clas NAUMANN, our dear departed friend, inspiration and mentor, to whose memory this paper is most respectfully dedicated. To him, gaining knowledge and understanding was always more important than merely accumulating information.

Acknowledgements. We are most grateful for the skilful and painstaking assistance of Ottmar Fischer (FZI) with SEM and macro-photography of androconia and for his comments on the manuscript. We thank Julie Harvey, Kim Goodger, Phil Ackery, Tony Hoare (BMNH) and Gerardo Lamas (Lima) for help with various matters. Special thanks are also due to Shayleen James (BMNH), who prepared Figs. 12–14 with great care. Other original figures were provided by: 1–4 BMNH photo studio; 5 Tony Hoare; 6–9 RIVW.

Zusammenfassung. Die südamerikanische Nymphaliden-Gattung *Bia* Hübner, 1919, wurde für mehr als 150 Jahre von den meisten Lepidopterologen als Mitglied der Satyrinae betrachtet. Neuere Berichte zu Präimaginalstadien sowie DNA-Analysen haben jedoch gemeinsame Merkmale mit den Morphinae: Brassolini aufgedeckt. Untersuchungen der Flügelmuster und der androconialen Organe von *Bia*, hier erstmals im Detail vorgestellt, zeigen ungewöhnliche Merkmale, die sonst nur von Brassolinen bekannt sind. Insbesondere das büschelförmige posteriore androconiale Organ der Hinterflügel, das Palisaden bildet, stellt eine Synapomorphie für *Bia* und verschiedene andere Gattungen der Brassolini, inclusive *Caligo*, dar. Die Gattung *Bia* wird daher formal von den Satyrinae zu den Morphinae: Brassolini übertragen, als einzigem Taxon des Subtribus Biina Herrich-Schäffer, 1864, **stat. nov.**, zusammen mit Brassolina Boisduval, 1836, und Naropina Stichel, 1925.

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APPENDIX I

Classification the satyrine clade *sensu* EHRLICH (1958) and KUZNETZOV & STEKOLNIKOV (2001), within the Nymphalidae Rafinesque, 1815, following break-up of the Biinae *sensu* MILLER (1968). Despite various changes, the current system still owes much to Miller (see HARVEY 1991). However, Miller overlooked some potentially important genera that clearly belong here, such as *Penthema* Doubleday, 1848, and *Xanthotaenia* Westwood, 1858, and these need to be located (KIRCHBERG, 1942, firmly included *Xanthotaenia* in the Amathusiini). The Melanitini currently include *Melanitis*, *Cyllogenes*, *Gnophodes*, *Parantirrhoea*, *Bletogona* and *Manataria* (UÉMURA 1987; WAHLBERG et al. 2003; YOSHIMOTO 2003). In future it seems possible that the Amathusiini could be relocated within the Satyrinae, while the grouping as a whole will probably be expanded to subsume the Charaxinae Guenée, 1865, and the Calinaginae Moore, 1895 (WAHLBERG et al. 2003). The suggestion of FREITAS & BROWN (2004) that the Apaturinae Boisduval, 1840, also belong here is contradicted by current molecular evidence (BROWER 2000; WAHLBERG et al. 2003).

Type genera are given in square brackets (for further details regarding these generic names see http://www.nhm.ac.uk/entomology/butmoth/index.html). The family group names, authorities, dates and type genera are in accordance with the as yet unpublished 'GloBIS' system for the nomenclature and classification of the butterflies (LAMAS et al. 2000, in prep.). Note that there is currently no widely accepted sub-tribal system for the Amathusiini. The work of KIRCHBERG (1942) will be invaluable in trying to formulate any effective subdivision. PARSONS (1998) has suggested that *Morphopsis* Oberthür, 1880, *Taenaris* Hübner, 1819 (including *Morphotenaris* Fruhstorfer, 1893), *Hyantis* Hewitson, 1862, and *Faunis* Hübner, 1819, may form a subgroup (for which the oldest available family-group name would be Hyantina Röber, 1905 [*Hyantis* Hewitson, 1862]). The Discophorina Stichel, 1902, are recognised by BASCOMBE et al. (1999).

Note that YOSHIMOTO (2003), following MILLER (1968), incorrectly attributed the following family-group names to Miller: Melanitini, Mycalesina, Ypthimina and Coenonymphina. By following Miller, Yoshimoto also misattributed Lethina to Clark, 1948; Melanargiina to Verity, 1920; gave the original date for Satyrinae Boisduval incorrectly as 1836; and misspelled Antirrheini as "Antirrhini". (Antirrhini Miller, 1968, is an objective synonym and homonym of Antirrhaeidi Reuter, 1896, the latter based on Westwood's invalid emendation "*Antirrhaea*"—see COWAN 1970—and which is properly corrected to Antirrheini Reuter, 1896, or Antirrheina Reuter, 1896, depending on adopted rank.)

- MORPHINAE Newman, 1834 [*Morpho* Fabricius, 1807]
  - MORPHINI Newman, 1834 [*Morpho* Fabricius, 1807]
    - ANTIRRHEINA Reuter, 1896 [*Antirrhea* Hübner, 1822]
    - MORPHINA Newman, 1834 [*Morpho* Fabricius, 1807]
  - BRASSOLINI Boisduval, 1836 [*Brassolis* Fabricius, 1807]
    - BIINA Herrich-Schäffer, 1864 [*Bia* Hübner, 1819] **stat. nov.**
    - NAROPINA Stichel, 1925 [*Narope* Doubleday, 1849]
    - BRASSOLINA Boisduval, 1836 [*Brassolis* Fabricius, 1807]
  - AMATHUSIINI Moore, 1894 [*Amathusia* Fabricius, 1807]

- SATYRINAE Boisduval, 1833 [*Satyrus* Latreille, 1810]
  - HAETERINI Herrich-Schäffer, 1864 [*Haetera* Fabricius, 1807]
  - MELANITINI Reuter, 1896 [*Melanitis* Fabricius, 1807]
  - ELYMNIINI Herrich-Schäffer, 1864 [*Elymnias* Hübner, 1818]
    - LETHINA Reuter, 1896 [*Lethe* Hübner, 1819]
    - ZETHERINA Reuter, 1896 [*Zethera* C. Felder, 1861]
    - ELYMNIINA Herrich-Schäffer, 1864 [*Elymnias* Hübner, 1818]
    - MYCALESINA Reuter, 1896 [*Mycalesis* Hübner, 1818]
  - ERITINI Miller, 1968 [*Erites* Westwood, 1851]
  - RAGADIINI Herrich-Schäffer, 1864 [*Ragadia* Westwood, 1851]
  - SATYRINI Boisduval, 1833 [*Satyrus* Latreille, 1810]
    - HYPOCYSTINA Miller, 1968 [*Hypocysta* Westwood, 1851]
    - YPTHIMINA Reuter, 1896 [*Ypthima* Hübner, 1818]
    - EUPTYCHIINA Reuter, 1896 [*Euptychia* Hübner, 1818]
    - COENONYMPHINA Tutt, 1896 [*Coenonympha* Hübner, 1819]
    - MANIOLINA Grote, 1897 [*Maniola* Schrank, 1801]
    - EREBIINA Tutt, 1896 [*Erebia* Dalman, 1816]
    - DIRINA Verity, 1953 [*Dira* Hübner, 1819]
    - PRONOPHILINA Reuter, 1896 [*Pronophila* Doubleday, 1849]
    - SATYRINA Boisduval, 1833 [*Satyrus* Latreille, 1810]
    - MELANARGIINA Wheeler, 1903 [*Melanargia* Meigen, 1828]

Bonner zoologische Beiträge	Band 53 (2004)	Heft 1/2	Seiten 255–282	Bonn, Juni 2005

Revision of the *vincta* Species-group of *Monolepta* Chevrolat, 1837 from Africa, Arabia and the Near East (Coleoptera: Chrysomelidae, Galerucinae)*[1]

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Abstract. Specimens of *Monolepta* Chevrolat, 1837 from Africa, the Arabian Peninsula and the Near East, which are characterized by yellow elytra with transverse black bands at base and in the apical third, are revised. This coloration is typical for most specimens of *M. vincta* Gerstaecker, 1871, a widely distributed and the most abundant species of *Monolepta* in Africa. Nine junior synonyms of this species could be found: *M. alternata* Chapuis, 1879, **syn. n.**; *M insignis* Weise, 1903, **syn. n.**; *M. sjöstedti* Weise, 1909, **syn. n.**; *M. ugandaensis* Laboissière, 1920, **syn. n.**; *M. lusingensis* Laboissière, 1920, **syn. n.**; *M. bouvieri* Laboissière, 1920, **syn. n.**; *M. striola* Laboissière, 1920, **syn. n.**; *M. consociata* Laboissière, 1920, **syn. n.**; *M. rugifrons* Laboissière, 1920, **syn. n.**; *M. femoralis* Laboissière, 1940, **syn. n.** Further species herein revised are *M. melanogaster* (Wiedemann, 1823) (= *M. bizonata* Chevrolat, 1837, **syn. n.**); *M. buquetii* Chevrolat, 1837; *M. lepida* Reiche, 1858. Newly described species are *M. sharonae* **sp. n.**, *M. ronbeeneni* **sp. n.**, and *M. naumanni* **sp. n.** Lectotypes are herein designated for: *M insignis* Weise, 1903; *M. sjöstedti* Weise, 1909; *M. lusingensis* Laboissière, 1920; *M. femoralis* Laboissière, 1940. Distribution maps and an identification key for these species are given.

Key words. Afrotropical region, Arabian Peninsula, Israel, taxonomy, biogeography, synonyms, lectotype, new species

1. INTRODUCTION

In the last catalogue of the Galerucinae (WILCOX 1973), 180 species of *Monolepta* Chevrolat, 1837 from tropical Africa were listed. Most of these species were described between 1890 and 1950 (WAGNER 2003a). With very few exceptions, the descriptions by preceeding authors were based on external characters only. The allocation to *Monolepta* and other genera of the "Monoleptites" (WILCOX 1973) was mostly typological. In an ongoing revision of this group, the afrotropical species of *Monolepta* turned out as polyphyletic, and many species need to be transferred to other groups (WAGNER 2004). Many synonyms particularly in widely distributed species, but also many undescribed species could be found (WAGNER 2000a, b; 2001, 2002, 2003b).

In this paper, afrotropical *Monolepta,* which have yellow to yellowish-red elytra, usually two transverse black elytral bands at base and in the apical third, are revised. Head and prothrorax are mostly yellow to red, rarely black; abdomen is yellow, in a few species sometimes entirely black or rarely only last abdominal segments black. The revision includes the most abundant afrotropical *Monolepta* species, *M. vincta,* which is described from Mombasa, Kenya. Wide distribution, high abundance and the high polymorphic coloration have led to a high number of synonyms. A further two species of this coloration type have been listed in the Dejean catalogue by CHEVROLAT (1837), *M. buquetii* from Senegal and *M. bizonata* from the Cape of Good Hope. The latter could be identified as a junior synonym of *M. melanogaster* described by WIEDEMANN (1823) also from the Cape of Good Hope using specimens with entirely black abdomen. The fourth valid species is *Monolepta lepida* described by REICHE (1858) from Palestine, a species which occurs also throughout the Arabian Peninsula and in northeastern Africa. Since the original description of most species are very short and lack the description of genitalic patterns, redescriptions are given for all species. *Monolepta buquetii* was never described, but there exist an indication in the Dejean catalogue only. Finally, three species with this peculiar coloration are described as new.

2. METHODS

A standard set of figures is given for each species. These include illustrations of the coloration (dorsal view), including the right antenna, where black coloration is indicated by black, yellow coloration by white, red coloration by dot-shading, and brown by black shading. The basal four antennal articles of two different males and females, dorsal and lateral view of the median lobe including the endophallic structures, and ventral view of the median lobe without the endophallic structures (for classification see WAGNER 2000), the spermathecae of three (if available) different females, and bursa-sclerites usually of one female are figured.

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* Revision of afrotropical *Monolepta* Chevrolat, 1837 – Part V. 19th contribution to the taxonomy, phylogeny and biogeography of afrotropical Galerucinae

[1] In commemoration of Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004)

Morphometric measurements were made for external characters. Absolute measurements are: Total length from the clypeus to apex of the elytron, length of elytron, maximal width of both elytra (usually in the middle or posterior third of the elytra), and width of pronotum. Relative measurements are: Length to width of pronotum, maximal width of both elytra to length of elytron, length of second to third antennomere, and length of third to fourth antennomere. The number of specimens measured is given in the description under "total length".

3. MATERIAL

The subsequent redescriptions and descriptions are based on labelled specimens from the following collections. Acronyms used and responsible curators in brackets: Bishop Museum, Honolulu (BPBM; A. Samuelson); The Natural History Museum, London (BMNH; S. Shute, M. Brendell, M. Cox); private collection Ron Beenen, Nieuwegein, The Netherlands (CBe); private collection Jan Bezdek, Brno, Čech Republic (CBz); private collection Manfred Döberl, Abensberg, Germany (CDö); private collection Uwe Heinig, Berlin, Germany (CHe); private collection Horst Kippenberg, Herzogenaurach, Germany (CKi); private collection Joachim Mauser, Germany (CMa); private collection Vladimir Medvedev, Moscow, Russia (CMe); Deutsches Entomologisches Institut, Müncheberg (DEI; L. Behne, L. Zerche); Hungarian Museum of Natural History, Budapest (HNHM; O. Merkl); Instituto de Investigação Científica Tropical, Lisboa (IICT; L. F. Mendes); Institute Royal des Sciences Naturelle de Belgique, Brussels (IRSNB; M. Cludts, D. Drugmand); Museo Civico di Storia Naturale, Genova (MCSN; R. Poggi); Museu de Catalunya, Barcelona (MCTB; G. Masó); Museo ed Instituto di Zoologia Sistematica, Universitá di Torino (MIZT; M. Daccordi); Musée National d'Histoire Naturelle, Paris (MNHN; N. Berti); Museum für Naturkunde der Humboldt Universität zu Berlin (ZMHB; J. Frisch, H. Wendt, M. Uhlig); Musée Royal d'Afrique Centrale, Tervuren (MRAC; M. de Meyer); Museum of Zoology, Helsinki (MZHF; H. Silfverberg); Museo Zoologico "La Specola", Firenze (MZUF; L. Bartolozzi); Naturhistorisches Museum Basel (NHMB; E. Sprecher-Übersax, M. Brancucci); Naturhistorisches Museum Wien (NHMW; H. Schönmann); Naturhistoriska Riksmuseet, Stockholm (NHRS; B. Viklund); National Museums of Kenya, Nairobi (NMK; W. Kinuthia, K. Maes); National Museum of National History, Washington (USNM; D. Furth); National Museum of Namibia, Windhoek (NMNW; E. Marais); Oxford University Museum of Natural History (UMO; G. McGavin); South African National Collection, Plant Protection Research Institute, Pretoria (SANC; E. Grobbelaar); South African Museum, Cape Town (SAMC; M. Cochrane); Transvaal Museum, Pretoria (TMSA; S. Gussmann); Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK; M. Schmitt, K. Ulmen); Zoological Institute St. Petersburg (ZISP; A. Kirejtshuk); Zoological Institute University of Kopenhagen (ZMUC; M. Hansen); Zoologisches Institut und Zoologisches Museum der Universität, Hamburg (ZMUH; R. Abraham).

For location data, geographical coordinates were given in degree and minute. These coordinates were mostly taken from the Alexandria Digital Library Gazetteer Server. Locations of the former Belgian Congo were in particular taken from a gazetteer compiled by Ugo Dall'Asta (MRAC).

4. REDESCRIPTIONS AND DESCRIPTION OF SPECIES

Monolepta melanogaster (Wiedemann, 1823)

= *Galleruca melanogaster* Wiedemann, 1823: 77.

= *Monolepta bizonata* Chevrolat, 1837: 407, **syn. n.**

Redescription.

Total length. 3.80–5.60 mm (mean: 4.81 mm; n = 12).

Head. Red, frons often yellowish-red (Fig. 1), about 15 % of specimens examined with dark brown or black vertex (Fig. 1a). Antennae pale yellow to reddish-yellow, last antennomere or its tip only brown, rarely black, antennomeres 4 to 10 about 4 times long than broad at apex. Length of antennomeres two to three 0.86–1.00 (mean: 0.96), length of antennomeres three to four 0.30–0.41 (mean: 0.35). Third antennomere particularly in large males very broad (Fig. 2a).

Thorax. Prothorax reddish-yellow (Figs 1a, b), in about 20 % of material examined yellow (Fig. 1c). Pronotal width 1.15–1.70 mm (mean: 1.42 mm), pronotal length to width 0.60–0.65 (mean: 0.63), very finely punctured. Elytra pale yellow to yellow with broad black base which is often smaller than in (Figs 1a, b) and can be reduced to broad black margins like in Fig. 1c in about 10 % of material examined, subapical elytral transverse black band usually broad, rarely smaller, but not reduced to a circular spot. Elytral length 2.90–4.20 mm (mean: 3.67 mm), maximal width of both elytra 1.90–2.85 mm (mean: 2.58 mm), maximal width of both elytra to length of elytron 0.68–0.72 (mean: 0.70). Scutellum red to yellowish-red. Meso- and metathorax, coxa, trochanter an basal two thirds of femur red to reddish-yellow, outer parts of legs yellow.

Abdomen. Yellow, in 12 % of material examined black.

Female genitalia. Spermatheca with spherical nodulus, comparatively broad middle part and cornu (Fig. 3).

Dorsal part of bursa sclerites triangular (Fig. 4a), ventral part slender, outer margin serrate to undulate (Fig. 4b).

Male genitalia. Median lobe conical, straight, apical part lanceolate, slightly widened beyond apex, apical half with significantly visible short hairs (Fig. 5a). Tectum pointed, ventral groove parallel-sided, slender (Figs 5b, c). Dorsal pair median endophallic spiculae strong, slightly bent inwards, other median spiculae slender, straight, ventral spiculae separated in two portions, hooked at apex, two pairs of slightly curved lateral spiculae, both of same size and orientation (Fig. 1b).

Distribution. Widely distributed and abundant in southern Africa. In Central Africa northwards towards northeastern Congo and western Uganda (Fig. 6).

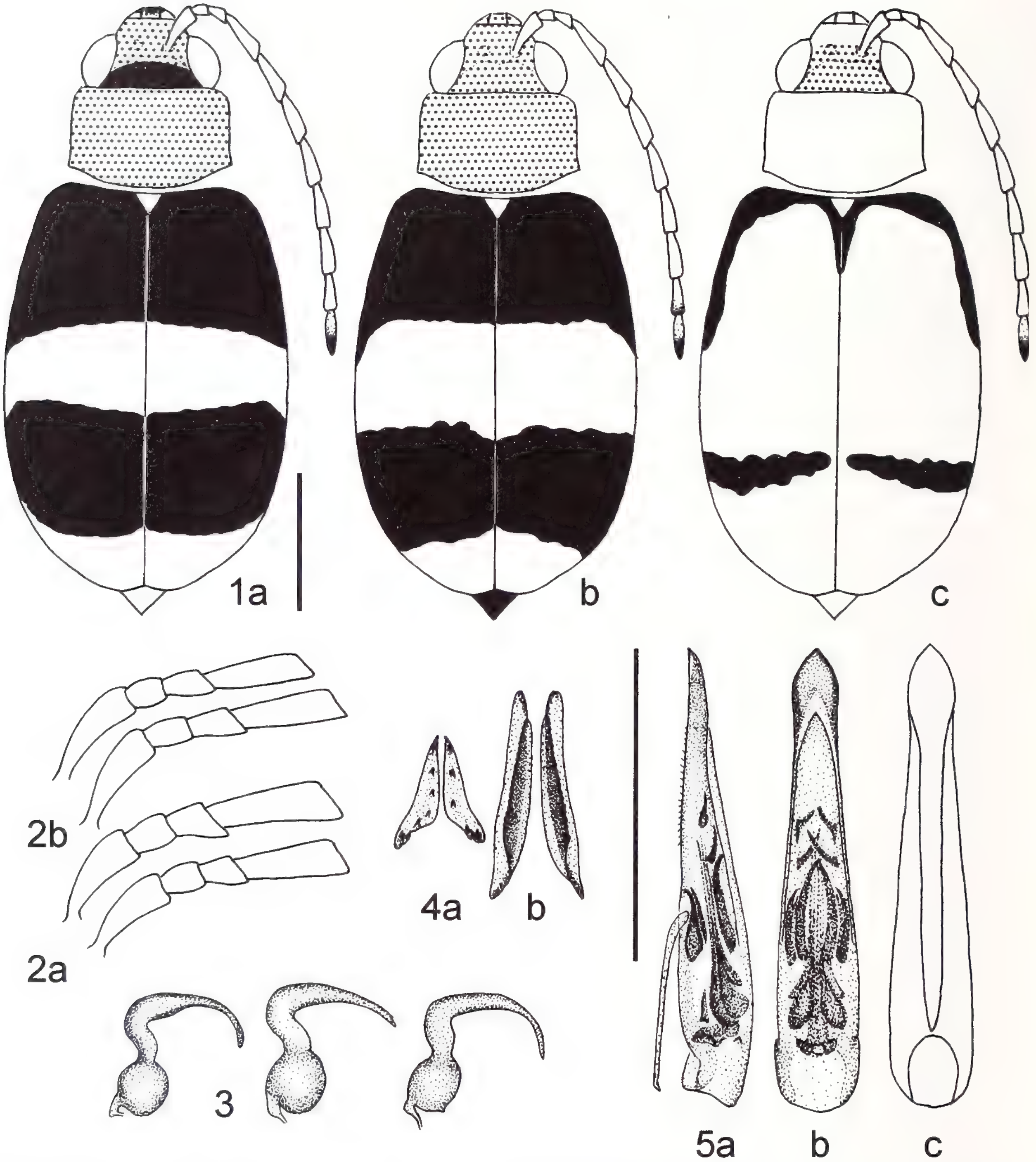
Diagnosis and discussion. On average the largest species of the coloration type is characterised by two transverse black bands. Specimens with a total length of more than 5 mm from Central or southern Africa belong to this species. Only some specimens of *M. lepida*, which is restricted to Somalia, Eritrea and Egypt, and occurs also in Arabia and the Near East, can be up to 5.5 mm. *Monolepta melanogaster* has shorter basal antennomeres than *M. lepida* (length of second to third antennomeres: 0.86–1.00, *M. lepida*: 0.75–0.88; length of third to fourth antennomeres: 0.30–0.41, *M. lepida*: 0.46–0.54), has a broader pronotum (pronotal length to width: 0.60–0.65; *M. lepida*: 0.63–0.67) and both species are allopatrically distributed.

Smaller specimens can be very similar to *M. vincta*, which is presumably most closely related to *M. melanogaster*. It can be distinguished on average by broader elytra (maximal width of both elytra to length of elytron: 0.68–0.72; *M. vincta*: 0.69–0.75), and shorter antennae. The median lobe is more homogeneously conical with slightly widened apex in *M. melanogaster* (Fig. 5b), while in *M. vincta* the apical part is more slender (Figs 23b, 24b). The endophallic armature of both species is very similar and only size and shape of the lateral spiculae show some constant differences (Figs 5b, 23b, 24b).

Some specimens can be hardly distinguished by external and genital morphology. Some doubt remains if these are two distinct species, a question which might be only solved by using molecular data. At this stage I prefer a specific differentiation supported mainly by geographic distribution, and variation of body size and colour pattern. From two locations, Garamba National Parc in north-eastern Congo, and Kibale Forest in western Uganda large series were collected. Both species occur syntopicly at these sites and seem to be genetically separated. *Monolepta vincta* shows high polymorphic coloration (Figs 18c, e) at this site, while *M. melanogaster* occurs only in one coloration type (Garamba Parc: Fig. 1c; Kibale Forest: Fig. 1b) and can be easily distinguished by significantly larger body size and by constant and comparatively high differences in male genital characters. This might be interpreted as character displacement of closely related distinct species when they occur syntopely. In South Africa and Namibia, and most parts of Zimbabwe, Zambia and southern Moçambique no specimens of "typical" *M. vincta* could be found and all specimens of the peculiar coloration type are assigned to *M. melanogaster*. In these countries many *M. melanogaster* are much smaller and on average of the same size as *M. vincta*. Only specimens from some populations, particularly from coastal areas of the Cape Region are larger.

Type material. Type specimens of *Galleruca melanogaster* Wiedemann, 1823 were not available, but species identity can be derived from the original description and several specimens from old collections bearing identification labels. – *Monolepta bizonata*. Holotype: ♀ "e. coll. Chev.^{t} / *Monolepta bizonata* Chev. C. b. Sp. Holotype" (BMNH); type locality: South Africa, Cape of Good Hope, 33.56S/18.28E. CHEVROLAT (1837: 407) listed this species in the third edition of the Dejean catalogue. The species was never described, but the name is available by indication (article 12.2, ICZN rules).

Further material examined. Angola: 1 ex., Tchivinguire, Huila, 15.00S/13.20E, XI.1974 (NMNW); 1 ex., Cahama, 15 km E, 16.18S/14.28E, XII.1974 (NMNW). – **Botswana:** 1 ex., Betchuanaland, Gaberones, 24.40S/25.55E, IX.1915, Ellenberger (MNHN); 1 ex., Serowe, XI.1985, P. Forchhammer (NMHB); 10, Serowe, VII.–IX.1988, P. Forchhammer (SANC). – **Burundi:** 1 ex., Bururi, 3.58S/29.35E, P. Giraudin, ex coll. Breuning (MRAC). – **Congo:** 1 ex., Kasai, Kondué, 4.57S/23.31E, E. Luja (MRAC); 1 ex., Kisantu, 5.07S/15.05E, P. Goosens (MRAC); 1 ex., Amadi, 3.35N/26.47E, III.1913, van den Plas (MRAC); 1 ex., Malela, 2.28S/26.09E, XII.1913, L. Burgeon (MRAC); 1 ex., Albertville, 5.56S/29.12E, XII.1918, R. Mayné (MRAC); 3 ex. Haut-Uele, Moto, 2.27N/26.25E, 1920, IV.–V.1923, L. Burgeon (MRAC); 2 ex., Haut-Uele, Abimva, 3.09N/29.50E, V.–VII.1925, L. Burgeon (MRAC); 2 ex, Lomami, Kaniama, 7.34S/24.11E, 1931, R. Massart (MRAC); 1 ex., Equateur, 00.05S/18.14E, IV.1932, P. Hulstaert (MRAC); 1 ex., Eala, 0.04N/18.17E, IV.1936, Henrard (MRAC); 5 ex., Lukolela, 1.03S/17.12E, 1937, R. Massart (IRSNB); 5 ex., Bambesa, 3.28N/25.43E, IV.1937, I.1940, J. Vrijdagh (4 IRSNB, 1 MRAC); 1 ex., Bas Congo, Mayidi, 5.11S/15.09E, 1942, van Eyen (MRAC); 1 ex., Lusinga, 8.56S/27.12E, 1760 m, IV.1947, G. F. de Witte (IRSNB); 1 ex., Kalanga, 9.34S/27.08E, Grotte de Kakontwé, VIII.1948, N. Leleup (MRAC); 1 ex., Basoko, 1.14N/23.36E, IV.1948, L. G. Benoit (MRAC); 1 ex., Stanleyville, Yaolema, 0.43N/24.28E, IV.1949, R. Laurent (MRAC); 102 ex., P. N. Garamba, 3.40N/29.00E, several locations, V.1950, IX.–XII.1951, V.1952 (54 ex. IRSNB, 48 ex. MRAC); 1 ex., Tshuapa, Bokuma, 0.06S/18.42E, V.1952, P. Lootens (MRAC); 2 ex., Elisabethville, 11.40S/27.28E, I.1956–I.1957, Ch. Seydel (MRAC). – **Congo, Republic:** 1 ex., reg. de Brazzaville, 4.00S/15.00E, 1906, Dupey (MNHN). – **Malawi:** 6 ex., Blantyre, 15.47S/35.00E, 1910, Dr. J. E. S. Old (BMNH); 3 ex., Mlanje, 16.05S/36.29E, XII.1912, S. A. Neave (BMNH); 5 ex., 50 km N Zomba, Liwonde, 15.22S/35.22E, VIII.2000, L. Schmidt (ZFMK). – **Moçambique:**



Figs 1–5: *Monolepta melanogaster* (Wiedemann, 1823) 1: colour pattern; 2: basal antennal articles (a: ♂, b: ♀); 3: three different spermathecae; 4: bursa-sclerites (a: dorsal, b: ventral); 5: median lobe (a: lateral, b: dorsal, c: dorsal. Scale for colour pattern different from same scales for basal antennal articles and genital structures: each 1 mm. Same for all following figures.

1 ex., Beira, 19.49S/34.52E, (SAMC); 1 ex., Chibababa, Lower Buzi R., 19.52S/34.45E, XII.1906, C. F. M. Swynnerton (BMNH); 3 ex., Pomene, 22.59S/35.35E, V.1975, beaten, costal bush, A. Strydom (TMSA). – **Namibia:** 1 ex., Kapako, Okavango, 18.01S/21.22E, XII.1954 (NMNW); 1 ex., Andara, SE 1821 Ab, Kavango, 18.04S/21.27E, VIII.1971 (NMNW); 11 ex., Nyangana, Okavango, 18.00S/20.41E, I.1985, H. Roer (ZFMK); 5 ex., E-Caprivi, Katima Mulilo, 17.29S/24.17E, III.1992, U. Göllner, M. Uhlig, lux (ZMHB); 1 ex., Kavango, Mahango GR, 18.14S/-21.43E, X.1993, F. Koch (ZMHB); 2 ex., Popa falls, 18.07S/-21.34E, XII.1993, M. Uhlig (ZMHB); 1 ex., Okavango, Bagani, Popa falls, 18.07S/21.34E, I.1995, F. Kantner (CKa); 1 ex., Popa Camp, II.1998, U. Göllner (ZMHB). – **South Africa:** 3 ex., Cap b. Sp., 33.56S/18.28E, 1817, "*melanogaster* Wied.", Mus.

Westerman (ZMUC); 1 ex., ex coll. Laferté, „*Monolepta bizonata* Chevr.; C. B. Sp. Verraux" (BMNH); 1 ex., Cap Diege, coll. Haag, "*Monolepta* Er. / *bizonata* Chev." (DEI); 1 ex., coll. Clavareau, coll. Chapuis, "*Monolepta pulchella* Klug / *Monolepta duplicata* Sahlb. = *pulchella* 1, Klug (MRAC); 1 ex., Cape Colony, coll. Clavareau, *Monolepta pulchella* Klug, Determinat Jacoby (MRAC); 2 ex., "*Galleruca atrofasciata* Diege Cap" (Halle); 1 ex., "*alternans*, N, *Crio. bifasciata*, Fab.?, Krebs, Pr. B. Sp., Lichtenst. / 30377 (ZMHB); 8 ex., Cap, ex coll. J. Weise (ZMHB); 1 ex., Cap, coll. de Bonvouloir (MNHN); 4 ex., P. B. Sp. (UMO); 1 ex., Cap B. Spei, Victoria (NHRS); 1 ex., Cape Town, coll. Jacoby (BMNH); 2 ex., Alexandria, Dorn Nek, J. L. Drege (SAMC); 5 ex., Caffraria, J. Wahlberg (NHRS); 1 ex., Caffra, coll. Fry (BMNH); 2 ex., Capland, Willamore, Dr. Brauns (BMNH); 3 ex., Kapland (ZMHB); 1 ex., Dunbrody, Cape Colony, 33.28S/25.33E, coll. Jacoby (BMNH); 4 ex., Transvaal, Fruhsdorfer (ZMHB); 4 ex., Transvaal (BMNH, MNHN, ZMHB, ZMUH); 6 ex., Transvaal, Lydenburg, 25.06S/30.27E, F. Wilms (ZMHB); 4 ex., Transvaal, Lydenburg (IRSNB); 1 ex., Transvaal, Pietersburg (BMNH); 1 ex., Grahamstown, 33.17S/26.32E, C. le Doux (ZMHB); 5 ex., Barberton, 25.48S/31.03E, P. Rendaff (BMNH); 4 ex., Natal (1 BMNH, 3 MNHN); 1 ex., Natal, Marshall, Jacoby coll. (BMNH); 4 ex., Natal, Estcourt, 29.00S/29.53E (SAMC); 1 ex., Natal, Frere, 28.53S/29.46E (SAMC); 1 ex., Wydah, R. P. Ménager (MNHN); 1 ex., Port Natal, 28.30S/30.30E, Boheman (ZMHB); 3 ex., Zoutpansberg, 28.10S/32.15E, Shilouvane, Junod, coll. Clavareau (MRAC); 1 ex., Port Elisabeth, 33.50S/25.45E, 1882, S. D. Bainslow, "*Monolepta bifasciata*, named 1899 by M. Jacoby" (UMO); 2 ex., Natal, Frere, 28.53S/29.46E, VI., X.1892, G. A. K. Marshall, on roses (BMNH); 11 ex., Natal, Estcourt, VIII.–X.1892, IX., IX., XI.1896, G. A. K. Marshall (BMNH); 1 ex., Transvaal, Hammanskraal, 25.24S/28.16E, 1893, E. Simon (MNHN); 1 ex., Oranje FS, Mateles Pic, 2400 m, I.1896, J. Thode (ZMHB); 1 ex., Maritzburg, 29.38S/30.24, II.1896, P. Cregoe (MNHN); 6 ex., Natal, Malvern, 29.53S/30.55E, I.1896, II., VIII., X.1897, XII.1899, G. A. K. Marshall (BMNH); 1 ex., Natal, Umgeni, 29.48S/31.03E, VII.1897, G. A. K. Marshall (BMNH); 1 ex., C. Bon. Spei, 1900, coll. Fry (BMNH); 1 ex., Transvaal, Sterkfontein, 24.42S/30.15E, 1900, H. P. Thomasset (BMNH); 1 ex., Natal, Upper Tongaat, 29.34S/30.45E, Barwon, 1600 ft, X.1901, G. A. K. Marshall (BMNH); 1 ex., Lower Tugela, 29.14S/31.30E, X.1901, *Monolepta melanogaster* Wied. (SAMC); 1 ex., Natal, Lower Tugela, 1902, E. Reynolds (BMNH); 2 ex., Durban, 29.51S/31.01E, 1902, F. Muir (BMNH); 1 ex, Transvaal, Zoutpansberg, 28.10S/32.15E, XII.1907, Knothe (ZMHB); 1 ex., Escourt, Mrs. E. J. Turner, 1909 (BMNH); 1 ex., Natal, Nw. Hanover, 28.03S/29.39E, X.1914 (SANC); 4 ex., East London, 33.02S/27.54E, IX., XII.1915, 1923, R. Ellenberger (MNHN); 2 ex., Pietermaritzburg, Fort Napier, 29.38S/30.25E, 1919 (ZMHB) ; 7 ex., Transvaal, Piet Retief, 27.00S/30.49E, II.1920, feeding on petals of bean flowers (3 BMNH, 4 SANC); 1 ex., Natal, Durban, VIII.1920, A. F. J. Gedye (NMK); 1 ex., Umatata, Transkei, 31.35S/28.47E, II.–III.1923, R. E. Turner (BMNH); 4 ex., Port St. John, 31.25S/29.30E, Pondoland, IV., VII.1923, R. E. Turner (BMNH); 1 ex., Natal, Weenen, 2840 ft, 28.05S/30.06E, VII.–IX.1923, H. P. Thomasset (BMNH); 1 ex., Aliwal North, Cape Prov., 30.41S/26.42E, XII.1923, R. E. Turner (BMNH); 1 ex., Transvaal, Machadodorp, 25.40S/30.15E, IV.1926, M. Mossop (SANC); 4 ex., S. Zululand, Gingindhlovu, V.1926, R. E. Turner (BMNH); 1 ex., Zululand, Eshowe, 2853S/31.28E, Turner (BMNH); 2 ex., Natal, Drakensberg, 28.43S/28.53E, van Reenen (BMNH); 1 ex., Oranje FS, Harrismith, 28.17S/29.08E, III.1927, R. E. Turner (BMNH); 2 ex., Somerset East., Cape Prov., 32.43S/25.35E, IX.1930, R. E. Turner (BMNH); 1 ex., Natal NaFauresmith, 29.45S/25.19E, V.1932, Dr. Henrici (1 BMNH, 4 SANC); 7 ex., Natal, Dundee, 28.10S/30.13E, VIII.1932 (2 BMNH, 5 SANC); 4 ex., Katberg, E. Cape Prov., 32.32S/26.41E I.1933, R. E. Turner (BMNH); 1 ex., Bainskloof, 33.35S/19.08E IX.1938, L. D. Brongerama (NNML); 1 ex., Natal NP, 60m s Ladysmith, X.1938, L. D. Brongerama (NNML); 1 ex., Zululand Mkuzi, XII.1945, DDT killed (SANC); 2 ex., Pretorius Kop, X.1950, H. K. Munro (SANC); 1 ex., Schoemanskloof, E. T., VI.1951, H. K. Munro (SANC); 1 ex., Natal, Richmond, XII.1954, ex coll. Breuning (MRAC); 1 ex., Natal, Durban, I.1955, K. Mannonen (Helsinki); 3 ex., Natal, Indaleni, 29.54S/30.17E, X.1956, Rev. W. Hunt, ex coll. Breuning (MRAC); 1 ex., Natal, Southbroom, 30.55S/30.19E, VII.1956, ex. coll. Breuning (MRAC); 1 ex., Politzi, VII.1966, P. Pali. (SANC); 1 ex., 32 m SW Loius Trichardt, X.1966 (SANC); 1 ex., Cape Prov., Kei Bridge, 32.31S/27.58E, I.1970, Cl. Besnard (MRAC); 2 ex., Zululand, Ndugu GR, 26.55S/32.19E, IV.1970, C. Besnard (MRAC); 1 ex., Zululand, Hluhluwe GR, 28.05S/32.04E, IX.1970, O. Bourquin (TMSA); 2 ex., Transvaal, Debegeni Falls, 5 km SE Magoebaskloof, II.1973, A. Prinsloo & T. Bouweri (SANC); 1 ex., Transvaal, Tswane, III.1973, A. Prinsloo (SANC); 1 ex., Zululand, Dukuduku Forest, 28.22S/32.19E, IV.1974, S. Endrödy-Younga, indig. forest litter (TMSA); 1 ex., Zululand, Empangeni, 28.45S/31.54E, IV.1975, P. E. Reavel (TMSA); 5 ex., Zululand, St. Lucia, Mission Rock, 28.22S/32.35E, XII.1975, S. Endrödy-Younga, at black light (TMSA); 1 ex., Natal, St. Lucia Mission Rocks, 28.22S/32.25E, XII.1975, S. Endrödy-Younga, at uv-light (TMSA); 1 ex., Transvaal, Naboomspruit, Libertas, 24.27S 28.33E, XI.1976, C. G. E. Moolman (SANC); 1 ex., Natal, Nyala GR nr Empangeni, 28.42S/31.46E, VIII.1977, P. Reavell (SANC); 1 ex., Austenburg, Kloof, IV.1978, coll. M. Keeping (TMSA); 1 ex., Transvaal, Pretoria, 25.45S/28.12E, XII.1978, C. G. Moolman (SANC); 2 ex., Transvaal, Barberton, 25.48S/31.03E, III.1979, C. Moolman (SANC); 1 ex., Transvaal, Grahamstown, III.1979, G. L. Prinsloo (SANC); 2 ex., Transvaal, Mogol NR, Ellisras Distr, 23.58S/27.45E, XI.1979, II.1984, C. D. Eardley (SANC); 1 ex., Transkei, Dwesa Forest, 32.17S/28.50E, XII.1979, S. Endrödy-Younga, flowering *Acacia* (TMSA); 4 ex., Transvaal, Mogoto NR, Zebediela, 24.15S/29.13E, X.1979, III.1980, G. L. Prinsloo et al. (SANC); 1 ex., Percy Fyfe NR, 24.03S/29.09S, III.1980, C. Kok (SANC); 8 ex., Kwa-Zulu, lake Sibaya, E shore, 27.22S/32.43E, I.1981, C. D. Eardley (SANC); 1 ex., Natal, Nottingham Road, 29.22S/29.59E, I.1981, S. J. v. Tonder & C. Kok (SANC); 1 ex., Natal, Cape Vidal, 28.10S/32.32E, I.1981, R. G. Oberprieler (SANC); 1 ex., Transvaal, Pretoria, Roodeplaat, 25.41S/28.18S, I.1983, C. Moolman (SANC); 1 ex., Cape Province, Knysna, 34.02S/23.03E, XI.1983, R. Oberprieler (SANC); 1 ex., Natal, Ngoye Forest, 1984, inside cumbers (BMNH); 2 ex., Natal, Pietermaritzburg, Town Bush Forest, 29.36S/30.23E, II.1984, C. G. E. Moolman (SANC); 1 ex., Natal, Mt. Nhlosane nr Dargle, 1600 m, 29.33S/29.56E, II.1984, C. G. E. Moolman (SANC); 1 ex., Natal, Wembesi nr Estcourt, 29.04S/29.46E, II.1984, C. G. E. Moolman (SANC); 1 ex., Natal, Balgowan, 29.23S/30.20^{E}, II.1984, R. Oberprieler & C. G. E. Moolman (SANC); 3 ex., Franskraal distr., Suikerbosnandfarm, W. Cape, IX.1984, W. Wittmer (NHMB); 2 ex., Kogmanskloof, 200 m, Cape Prov., X.1984, W. Wittmer (NHMB); 1 ex., S. Cape Prov., Herbertsdale, 34.01S/21.46E, X.1984, R. Müller (TMSA); 5 ex., E Cape Prov., 35 km N Grahamstown, 32.57S/26.09E, X.1984, S. Endrödy-Younga, ground & vegetation (TMSA); 1 ex., Cape Province, Mitchell's Pass nr Ceres, 33.23S/19.27E, XI.1984, C. Eardley (SANC); 1 ex., Cape Province, Saasveld nr George, 33.57S/22.35E, II.1985, W. Breytenbach (SANC); 1 ex., S. Natal, Weza-Lovedale, 30.40S/29.41E, III.1985, S. Endrödy-Younga, sift. indig. for. litt. (TMSA); 1 ex., Transvaal, Messina, V.1985, Naudé (SANC); 1 ex., SW Cape, Clanwilliam, 32.09S/18.53E, IX.1985, on vegetation on flood plain (TMSA); 1, Transvaal, Letsitele, 23.52S/30.24E, X.1985, S. Kamburow (SANC); 1 ex., Transvaal, Bourkes Luck, 24.40S/30.48E, II.1986, C. D. Eardley (SANC); 1 ex., Transvaal, Loius Trichardt, 800 m,23.03S/29.49E, II,1986, D. d'Hotman (TMSA); 1 ex., E. Cape, Grahamstown, 33.19S/26.31E, VI.1886, S. van Noort (SAMC); 1 ex., Meiringspoort, 33.24S/22.33E, IX.1986, N. MacPherson (SAMC); 5 ex., Transvaal, Entabeni FR, 33.00S/30.16E, I.1987, C. D. Eardley (SANC); 1 ex., Transvaal, Hans Merensky NR, 23.42S/30.44E, I.1987, B. Grobbelaar (SANC); 5 ex., Transvaal, Swadini, Blydepoort NR, 24.32S/30.54E, I.1987, B. Grobbelaar (SANC); 1 ex., Transvaal, Modjadji NR, 23.38S/30.20E, I.1987, C. D. Eardley (SANC); 5 ex., Transvaal, Nelshoogte Knuckles Rocks Forest, 25.47S/30.50E, II.1987, S. Endrödy-Younga, beating in forest (TMSA); 1 ex., Transvaal, Uitsoek waterfall, 25.16S/30.33E, II.1987, S. Endrödy-Younga, beating (TMSA); 7 ex., OFS, Tussen Die Riviere Res. nr Bethulie, 30.30S/26.12E, III.-IV.1987, B. Grobbelaar (SANC); 2 ex., Transvaal, Wyllieespoort, Ingwe Motel, 22.58S/29.57E, II.1988, G. D. Butler (SANC); 1 ex., Transvaal, Kruger NP, Satara, 24.23S/31.46E, 350 m, II.1988, B. Grobbelaar (SANC); 2 ex., Transvaal, Meiringspoort, Groot Swartberge, 33.33S/22.19E, XI.1988, R. Oberprieler (SANC); 2 ex., Cape Province, Suurberg NR, 33.16S/25.45E, XI.1988, R. Oberprieler (SANC); 1 ex., Cape Province, Phanton Pass nr Knysna, 34.00S/22.59E, XII.1988, R. Oberprieler (SANC); 2 ex., Cape Province, Brenton-on-Sea, Knysna, 34.04S/23.01E, XII.1988, E. Grobbelaar (SANC); 3 ex., Transvaal, Barberton, 25.50S/31.02E, I.1988, E. Holm & E. Marais (NMNW); 1 ex., Natal, 27 km S Empangeni, 28.57S/31.43E, II.1989, B. Grobbelaar & E. v. d. Linde (SANC); 1, Gankapoordam, Cape Prov., VIII.1989, G. Minet (NHMB); 1 ex., 23 km N East London, IX.1989, W. Wittmer & S. Gussman (NHMB); 4 ex., Transkei, Port St. John, Silaka, 31.33S/29.30E, XI.–XII.1987, S. Endrödy-Younga, at uv-light (TMSA); 1 ex., Transvaal, Montrose State Forest, Barberton, 25.50S/31.02E, I.1988, E. Holm & E. Marais (NMNW); 1 ex., Transvaal, Uakhutswa River, Ofcolaco, 24.05S/30.22E, I.1989, Werner (cDö); 4 ex., Transvaal, Witpoortjie, Botanical Garden, 26.07S/27.50E, II.1989, B. Grobbelaar (SANC); 3 ex., Transvaal, Lekgalameetse NR, 24.10S/30.14E, II.1989, V. M. Uys / N. Verheijen (SANC); 6 ex., Natal, Cathkin Peak Hotel, 29.00S/29.27E, IV.1989, E. v. d. Linde (SANC); 1 ex., Natal, Overstone nr Fawn Leas Farm, 29.22S/30.36E, X.1989, E. v. d. Linde (SANC); 3 ex., Transvaal, Weltevreden Farm nr. Nelspruit, 25.34S/31.10E, II.1989, I.1990, R. Oberprieler, V. M. Uys (SANC); 2 ex., Natal, St Lucia Estuary, 28.17S/32.25E, II.1989, B. Grobbelaar & E. v. d. Linde (SANC); 1 ex., 20 km S Mkuze, 27.56S/32.13E, Natal, IX.1989, W. Wittmer & S. Gussmann (MNHB); 1 ex., Transvaal, Roodeplast dam nr Pretoria, 24.41S/28.18E, X.1989, J. S. Donaldson (SANC); 1 ex., Cape Province, Keurboomrivier Mond nr. Plettenberg Bay, 34.02S/23.24E, II.1990, M. Jonsson (SANC); 2 ex., Cape Province, Swartberg pass, 33.19S/22.03E, II.1990, M. Jonsson (SANC); 2 ex., Cape Province, Kango Mts Ressort nr Oudtshoorn, 33.31S/22.21E, II.1990, M. Jonsson (SANC); 2 ex., Beacon Bay, Cape Prov., X.1990, W. Wittmer (NHMB); 2 ex., 70 km W Grahamstown, X.1990, W. Wittmer (NHMB); 1 ex., Transkei, Lusikisiki, 31.21S/29.35E, XI.1991, Richter (MIZT); 2 ex., Pretoria, 25.45S/28.12E, XI.1992, W. Wittmer (NHMB); 1 ex., Wonderdal Farm, Graaff-Reinet, 32.15S/24.32E, 800 m, XI.1992, W. Wittmer (NHMB); 1 ex., Port Elisabeth, Addo Elephant NP, 30.50S/25.45E, XII.1992, F. Koch (ZMHB); 1 ex., Groenfontain, SW of Naboomsprui, 24.38S/28.31E, II.1993, E. Grobbelaar (SANC); 1 ex., Dragon Peaks Park, 1150–1450 m, 29.02S/29.26E, XI.1993, J. Deckert, lux (ZMHB); 4 ex., Natal, Drakensberg, 29.03S/29.24E, IX.1993, II.1994, U. Göllner, F. Koch (ZMHB); 6 ex., Natal, Itala GR, 27.30S/31.20E, I.1994, II.1995, U. Göllner, F. Koch (ZMHB); 1 ex., Natal, Spa ca. 20 km SES Paulpietersburg, 27.32S/30.57E, II.1994, U. Göllner (ZMHB); 1 ex., Natal, Sodwana Bay NP, 27.37S/32.41E, I.–II.1994, U. Göllner (ZMHB); 1 ex., Natal, Mkunza NP, 27.36S/32.13E, II.1994, F. Koch (ZMHB); 3 ex., KwaZulu-Natal, St. Lucia Park, 28.12S/32.25E, II.1995, F. Koch (ZMHB); 1 ex., KwaZulu-Natal, N`dumu GR, 26.55S/32.19E, II.1995, F. Koch (ZMHB); 1 ex., KwaZulu-Natal, Pongola River, Makanes Drift, 27.01S/32.18E, II.1995, F. Koch (ZMHB); 5 ex., Cape Prov., Citrusdal, Olifantsriver, 32.36S/19.08E, IV.1995, U. Göllner (ZMHB); 2 ex., Bontbok NP, 34.04S/20.27E, IV.1995, J. Deckert, U Göllner (ZMHB); 1 ex., KwaZulu-Natal, Sodwana Bay NP, 27.37S/32.41E, XI.1995, F. Koch (ZMHB); 1 ex., Bophutatswana, Pilansberg NP, 25.15S/27.13E, 1200–1500 m, XI.1996, M. Hartmann (NME); 3 ex., Legalameetse NR, Makhutsi Camp, 24.12S/30.18E, 1200 m, I.1997, E. Grobbelaar (SANC); 1 ex., Tshipise, Nonet NR, 22.37S/30.10E, 320 m, XI.1998, M. Hartmann (NME); 1 ex., Karoo, Graaf-reinet Camp, 32.14S/24.32E, 500 m, XI.-XII.1996, M. Hartmann (NME); 1 ex., W-Cape, Greyton, 34.03S/19.37E, X.1999, M. Snizek (MIZT). – **Uganda:** 1 ex., Tero Forest, SE Buddu, 0.50S/31.40E, IX.1911, S. A. Neave (BMNH); 1 ex., Bugiri, 0.34N/33.45E, 1400 m,VIII.1957, P. Basilewsky & N. Leleup (MRAC); 176 ex., Kibale Forest, 0.50N/31.06E, VII., IX.-X.1983, VI., IX.1984, IV.-V.1985, IX.1986, M. Nummelin (Helsinki); 2 ex., Ft. Portal, Kibale Forest, 0.45N/31.00E, V.–IX.1992, coll. Maus (ZFMK); 5 ex., Kibale Forest, Kanyaware, 1600 m,VII.-VIII.1998, L. Schmidt (ZFMK). – **Zambia:** 1 ex., Victoria Falls, 17.55S/25.51E, 3000 ft, IX.1905, B. E. Poulton (UMO); 11 ex., Victoria Falls, Palm Kloof, IX.1905, B. E. Longstaff (UMO); 1 ex., Lofu River, 8.34S/30.44E, 3500 ft, VIII.1909, S. A. Neave (UMO); 2 ex., Upper Luangwa, 14.49S/19.06E, 1880–2000 ft, III.1908, S. A.Neave (BMNH, UMO); 1 ex., Mid-Lungwa, 14.00S/19.00E, VIII.1910, S.A. Neave (BMNH); 1 ex., Niamadzi R., nr. Nawalia, VIII.1910, S. A. Neave (BMNH); 1 ex., Mwengwa, 13.00S/27.40E, VIII.1913, H. C. Dollman (BMNH). – **Zimbabwe:** 1 ex., Mashonaland, Jacoby coll. (BMNH); 2 ex., Matabele, Hård af Seg. (NHRS); 2 ex., Salisbury, 17.43S/31.05E, Jacoby coll. (BMNH, SAMC); 1 ex., Umchaki River, II.1897 (BMNH); 5 ex., Salisbury, II.1895,VIII.1898, II.1899, VI.–VII.1900, G. A. K. Marshall (BMNH); 6 ex., Salisbury, I., II., V., VIII.1898 (BMNH); 2 ex., Salisbury, VIII.1898, on *Mosasa*, Jacoby coll. (BMNH, SAMC); 1 ex., Old Umtali, 19.00S/32.40E, X.1897, G. A. K. Marshall (BMNH); 3 ex., Mashonaland, Chirinda, 20.05S/31.28E, X.1905, G. A. K. Marshall (BMNH); 1 ex., Selukwe, 19.40S/30.02E, 1915, A. Ellenberger (MNHN); 1 ex., near Fort Victoria, 20.10S/30.49E, IX.1931, J. Ogilvie (BMNH); 2 ex., Umtali, 19.00S/32.40E, Xmas Pass, V.1932, J. Ogilvie (BMNH); 1 ex., Imbezi Valley, III.1957, N. L. H. Krauss (BMNH); 1 ex., Melsetter, 19.48S/32.52E, 1700 m,VII.1960, N. Leleup (MRAC); 1 ex., Mpika, Muchinga Mts., 11.15S/31.27E, 1700 m, VII.1960, N. Leleup (MRAC); 1 ex., Khami ruins, Bulawayo, 20.15S/28.30E, 1350 m, XI.1987, W. Wittmer (NHMB); 1 ex., Kyle RP, Lake Mutirikwi, 20.13S/31.00E, XII.1993, F. Koch (ZMHB); 1 ex., Chimanimani, 19.47S/32.50E, XII.1998, S. Bečvář (CBz); 1 ex., 15 km SE of Muzarabani, 16.20S/31.10E, XII.1998, S. Bečvář (CBz).

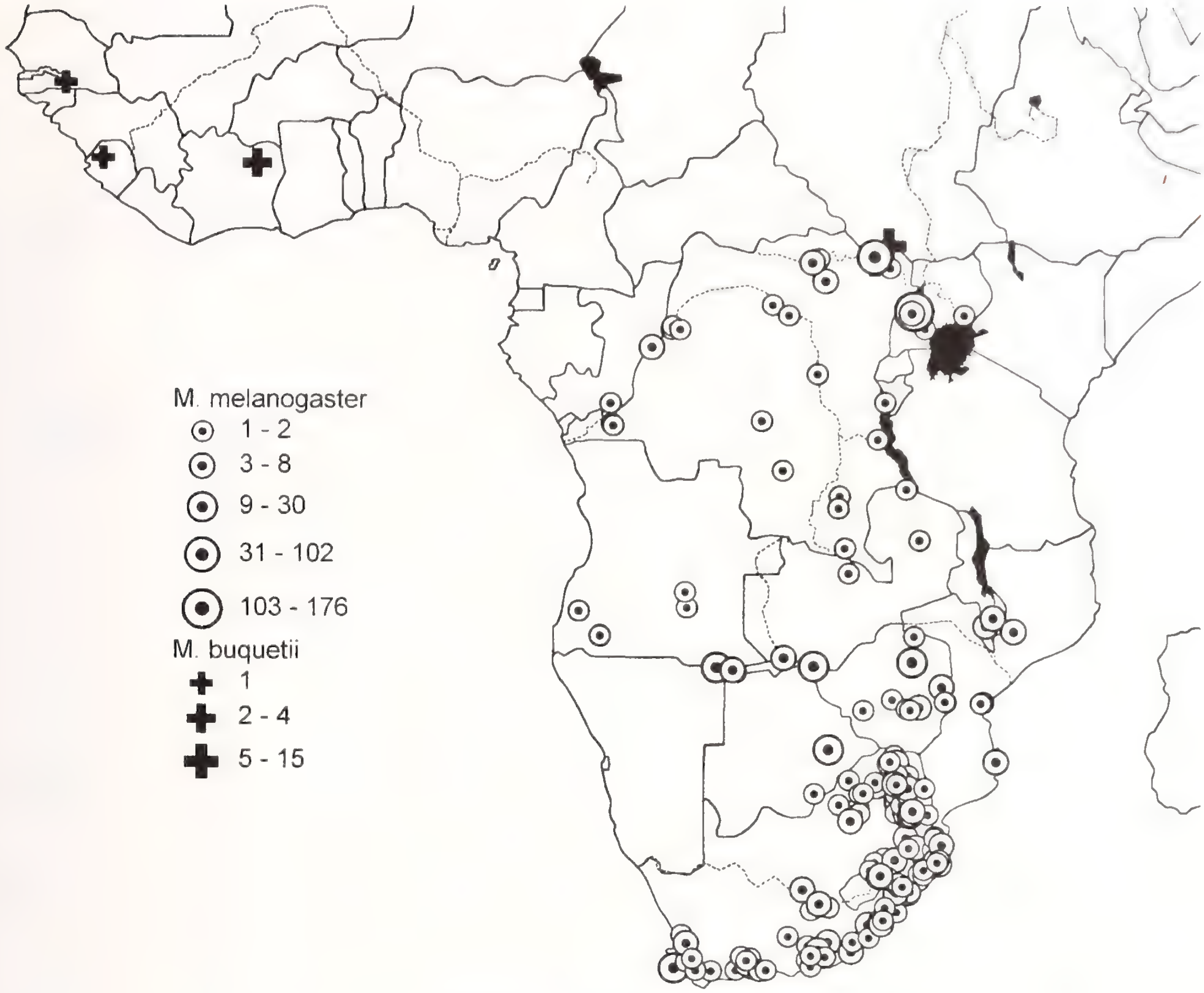


Fig. 6: Distribution of *Monolepta melanogaster* (Wiedemann, 1823), and *M. buquetii* Chevrolat, 1837

Monolepta buquetii Chevrolat, 1837

Description.

Total length. 3.00–4.20 mm (mean: 3.58 mm; n = 8).

Head. Including mouth parts yellowish-red, in some specimens labrum and frons yellow, vertex yellowish-red, vertex very broad (Fig.7). Antennae pale yellow throughout, rarely tip of last antennomere dark brown, antennomeres four to eleven short, less than 4 times long than broad at apex, third antennomere very short in males (Fig. 8a), more elongated in females (Fig. 8b). Length of antennomeres two to three 1.00–1.40 (mean: 1.17), length of antennomeres three to four 0.20–0.36 (mean: 0.30).

Thorax. Prothorax entirely pale yellow. Pronotal width 0.95–1.20 mm (mean: 1.11 mm), pronotal length to width 0.54–0.58 (mean: 0.57), pronotum very finely punctured. Elytra pale yellow with narrow transverse black band at base, and each elytron with transverse black spot in the apical third, often much smaller than in Fig. 7a. Rarely elytra with broad black basal and outer margins reaching towards the apical third and sometimes joining with the subapical spot (Fig. 7b). Elytral length 2.55–3.15 mm (mean: 2.68 mm), maximal width of both elytra 1.60–2.10 mm (mean: 1.92 mm), maximal width of both elytra to length of elytron 0.69–0.73 (mean: 0.72). Scutellum yellow. Meso- and metathorax reddish-yellow, legs completely pale yellow.

Abdomen. Yellow to reddish-yellow.

Female genitalia. Spermatheca with spherical nodulus, comparatively broad middle part and short, slender cornu (Fig. 9). Dorsal part of bursa sclerites with narrowed, hook-like base (Fig. 10a), ventral part slender, outer margin very finely serrate (Fig. 10b).

Male genitalia. Median lobe very slender in the apical half (Fig. 11), apex usually rounded (Figs 11b, d), rarely pointed (Fig. 11c). Tectum and ventral groove of median lobe narrow (Figs b, c). One pair of median endophallic spiculae strong, significantly bent at apex, ventral spiculae slender, apically hooked, lateral spiculae very small, triangular (Fig. 11b).

Distribution. Known from savannas of West and northern Central Africa (Fig. 6).

Diagnosis. *Monolepta buquetii* is one of the smallest *Monolepta* species known from Africa. Size and coloration is most similar to *M. vincta* and *M. sharonae* sp. n. Males can be easily distinguished by the very short third antennomere (Fig. 8a). Generally, short antenna, broad head and the transverse pronotum are good external, and shape of median lobe and spermatheca are excellent genital diagnostic characters of *M. buquetii*.

Type material. Holotype: ♂ "E. Coll. Laferté / *Monolepta Buquetii* Dj. Senegal / Holotype" (BMNH); type locality: Senegal. CHEVROLAT (1837: 407) listed this species in the third edition of the Dejean catalogue. It was not described, but the name is available by indication (article 12.2, ICZN rules).

Further material examined. Congo: P. N. Garamba, 3.40N/29.00: 4 ex., I/a/1, I/b/3, I/c/1, I.–II.1950, H. de Saeger (2 ex. IRSNB, 2 ex. MRAC); 5 ex., I/a/1, I/b/1, II., IX.1950, G. Demoulin (IRSNB); 1 ex., II/fc/18, XI.1951, H. de Saeger (IRSNB); 1 ex., II/gd/4, III.1952, H. de Saeger (IRSNB); 2 ex., PFSK.25/3, VI.1952, H. de Saeger (IRSNB); 12 ex., P. N. Garamba, Ndelele, 4.22N/29.47E, II.–III., VII.1952, H. de Saeger (8 ex. IRSNB, 4 ex. MRAC); 2 ex., 2/source, VI.1952, H. de Saeger (IRSNB). – **Ivory Coast:** 4 ex., Comoé NP, 8.75N/3.80W, VI.–VII.1997, C. Mody (ZFMK). – **Senegal:** 1 ex., Guede, II.1946 (BMNH).

Monolepta lepida Reiche, 1858

Redescription.

Total length. 3.80–5.30 mm (mean: 4.68 mm; n = 10).

Head. Pale yellowish-red (Fig. 12a), frons sometimes yellow (Fig. 12b). Antennae pale yellow, tip of terminal antennomere black, antennomeres four to eleven about 4 times longer than broad at apex. Basal antennomeres elongated, third antennomere significantly longer than second particularly in males (Fig. 13a), length of antennomeres two to three 0.75–0.88 (mean: 0.84), length of antennomeres three to four 0.46–0.54 (mean: 0.49).

Thorax. Prothorax pale yellow to yellowish-red (Fig. 12). Pronotum narrow, width 1.10–1.55 mm (mean: 1.33 mm), pronotal length to width 0.63–0.67 (mean: 0.66), very finely punctured. Elytra pale yellow, base with narrow transverse black band (Fig. 12a), rarely black coloration reduced to spots at humeri (Fig. 12b), subapical transverse elytral band narrow. Some specimens from Oman have a yellowish-red head, pronotum and elytra with larger, more circular subapical elytral spots. Elytral length 2.80–3.80 mm (mean: 3.41 mm), maximal width of both elytra 2.00–2.70 mm (mean: 2.34 mm), maximal width of both elytra to length of elytron 0.65–0.70 (mean: 0.68). Scutellum yellow to yellowish-red. Meso-, metathorax, and legs usually yellow, rarely yellowish-red, but tibia and tarsus always pale yellow.

Abdomen. Pale yellow to yellow.

Female genitalia. Spermatheca with spherical nodulus, comparatively broad middle part and cornu (Fig. 14). Dorsal part of bursa sclerites slender, with row of hooks at base (Fig. 15a), ventral part very slender, outer margin very finely serrate (Fig. 15b).

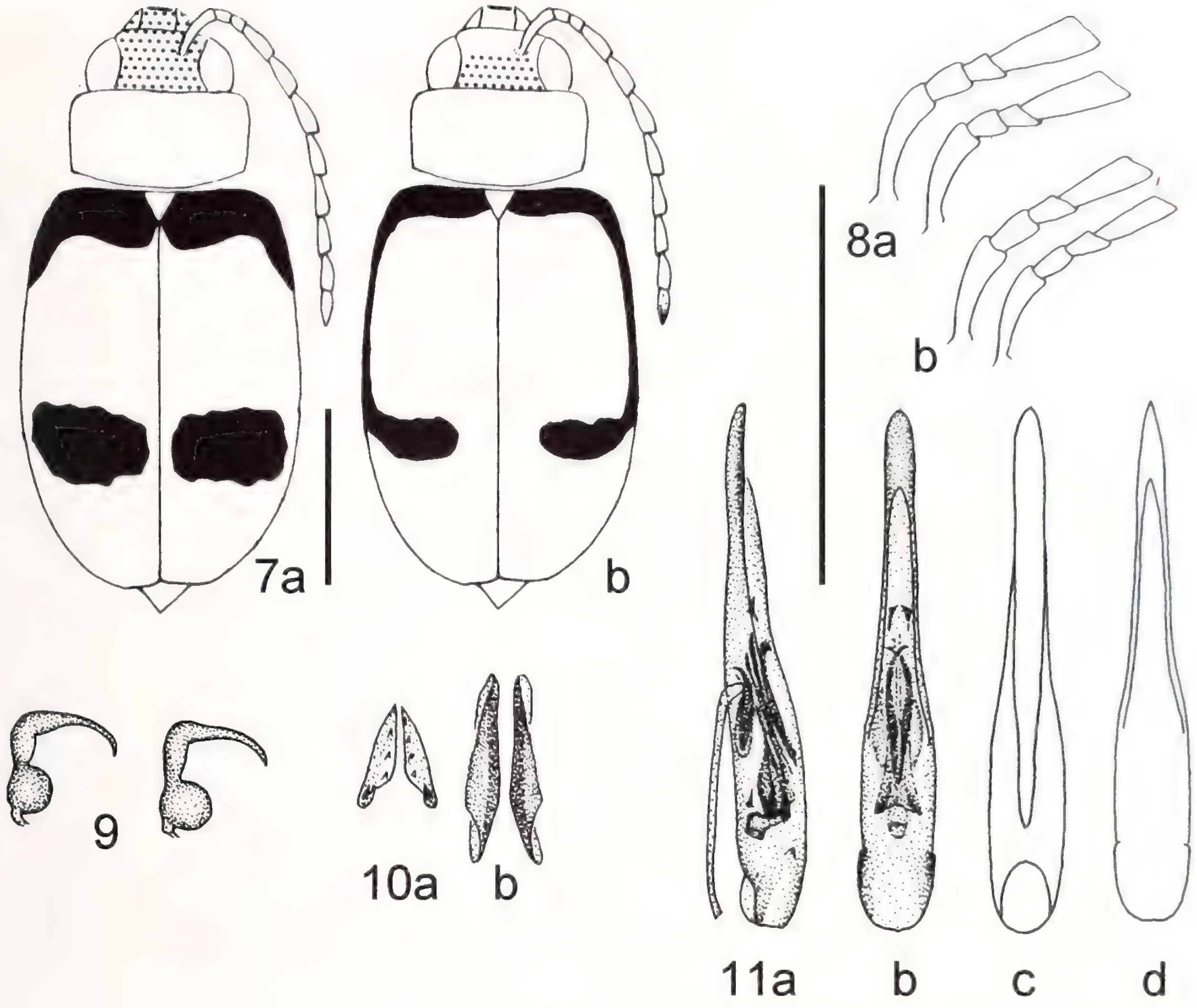
Male genitalia. Median lobe conical, straight, apical part spoon-like widened (Fig. 16a), ventrally bent (Fig. 16b). Tectum slender, pointed, ventral groove parallel-sided, very slender (Fig. 16c). Dorsal pair of median endophallic spiculae stronger, very long, other median spiculae slender, long, ventral spiculae separated in two portions, hooked at apex, lateral spiculae slender, long, bifurcate (Figs 16a, b).

Distribution. Most specimens are known from the Arabian Peninsula and this species reaches the Palaearctic Region in Israel and Jordan. A few specimens are known from Eritrea and Somalia (Fig. 17), and occurs most likely also in Egypt and eastern Sudan.

Diagnosis. Most similar to *M. vincta* and both species occur sympatrically in north-east Africa. Including *M. melanogaster*, these three species are most likely a monophyletic group, which can be derived from external characters, coloration, and male genital patterns, particularly the type of the endophallic armature. In comparison to *M. vincta*, *M. lepida* is on average larger, and has reduced black elytral coloration, while syntopic *M. vincta* often has broad transverse black elytral bands. Good diagnostic external characters are the elongated second and third antennomeres in *M. lepida* (length of second to third antennomeres: 0.75–0.88, *M. vincta*: 0.86–1.00; length of third to fourth antennomeres: 0.46–0.54, *M. vincta*: 0.27–0.35) and the narrow pronotum (pronotal length to width: 0.63–0.67, *M. vincta*: 0.57–0.64).

Type material. Holotype: ♀ "Vog. de Saulcy, Jerusalem / *Monolepta lepida* Reiche 1858 / Muséum Paris 1952 coll. R. Oberthur / Holotype" (MNHN); type locality: Israel, Jerusalem, "des bords du Jourdain" which is about 30 km east of the centre of Jerusalem. REICHE (1858) gave a detailed description of external characters and coloration including an excellent figure (pl. 1, fig. 10). His description based most likely on a single specimen "M. Azambre, à qui dois un bel individu de cette espéce, ..." which is considered as holotype. The original description was repeated in JOANNIS (1866).

Further material examined. Eritrea: 2 ex., Agorgat, 15.33N/37.53E, I.1906, D. Figini (MCSN); 23 ex., Assab, 13.00N/42.44E, 1907, Katona (HNHM). – **Israel:** 2 ex., Wadi Arugod, Ein Gedi,



Figs 7–11: *Monolepta buquetii* Chevrolat, 1837 7: colour pattern; 8: basal antennal articles (a: ♂, b:); 9: two different spermathecae; 10: bursa-sclerites (a: dorsal, b: ventral); 11: median lobe (a: lateral, b: dorsal, c: dorsal, variation with pointed apex, d: ventral, without endophallic structures).

31.27N/35.23E, III.1963, W. Wittmer (CMe). – **Jordan:** 1 ex., Wadi Schaib, 30.30N/36.00E, 100 m, XI.1959, J. Klapperich (NHMB). – **Oman:** 7 ex., Dhofar, 17.00N/54.10E, X.1979, T. B. Larsen (NHMB); 1 ex., Dhofar, Ain Rzat, Salalah, 17.01N/54.06E, II.1989, W. Wittmer (NHMB); 2 ex., 30 km W Salalah, Wadis nr. Al Mughsayi, 17.00N/53.50E, II.1998, G. Wewalka (NHMB). – **Saudi Arabia:** 1 ex., Jebel Ibrahim, 20.25N/41.11E, 1540 m, VIII.year?, W. Büttiker (NHMB); 3 ex., Shileam, XI.1935, R. C. M. Darling (BMNH); 2 ex., Wadi Johan, Abha, 18.12N/42.30E, 2150 m, IV.1976, Wittmer & Büttiker (NHMB); 1 ex., Wadi ad Dilla, 1120 m, X.1979, W. Büttiker (NHMB); 1 ex., Al Alayyah, 19.36N/41.58E, 1950 m, X.1979, W. Büttiker (NHMB); 6 ex., Thanomah, 1950 m, IV.1980, W. Büttiker (1 CMe, 5 NHMB); 1 ex., Riyadh, 24.40N/46.43E, V.1980, W. Büttiker (NHMB); 2 ex., An Nimas, 19.07N/42.08E, VII.1981 (CMe); 1 ex., Jizan, 16.57N/42.33E, III.1984, A. S. Talhouk (NHMB); 1 ex., Bani Rizam, 18.20N/42.28E, 2230 m, IX.1984, W. Büttiker (CMe); 1 ex., Harithi, 21.18N/40.18E, IV.1985, W. Büttiker (NHMB). – **Somalia:** 1 ex., Br. Somaliland, 10.00N/48.00E, B.M. 1929-398, W. A. Macfadyen (BMNH); 1 ex., Burao, Br. Somaliland, 9.00N/46.00E, VII.1942, J. R. Audy (BMNH); 3 ex., Run, Garee, VIII.1964, Miss. Biol. (NHMB); 5 ex., Run, 8.47N/48.56E, VII.1969 (NHMB); 1 ex., Taleh, 9.09N/48.26E, IV.1980 (NHMB). – **Yemen:** 2 ex., Jebel Jihaf, Wadi Leje, 13.45N/44.42E, 6300–6700 ft, X.1937, Scott & Britton (BMNH); 1 ex., Wadi Natid, Kirsh, 13.22N/44.32E, 2300 ft, XII.1937, Scott & Britton (BMNH).

Monolepta vincta Gerstaecker, 1871: 83

= *Monolepta alternata* Chapuis, 1879: 23; **syn. n.**

= *Monolepta insignis* Weise 1903: 212; **syn. n.**

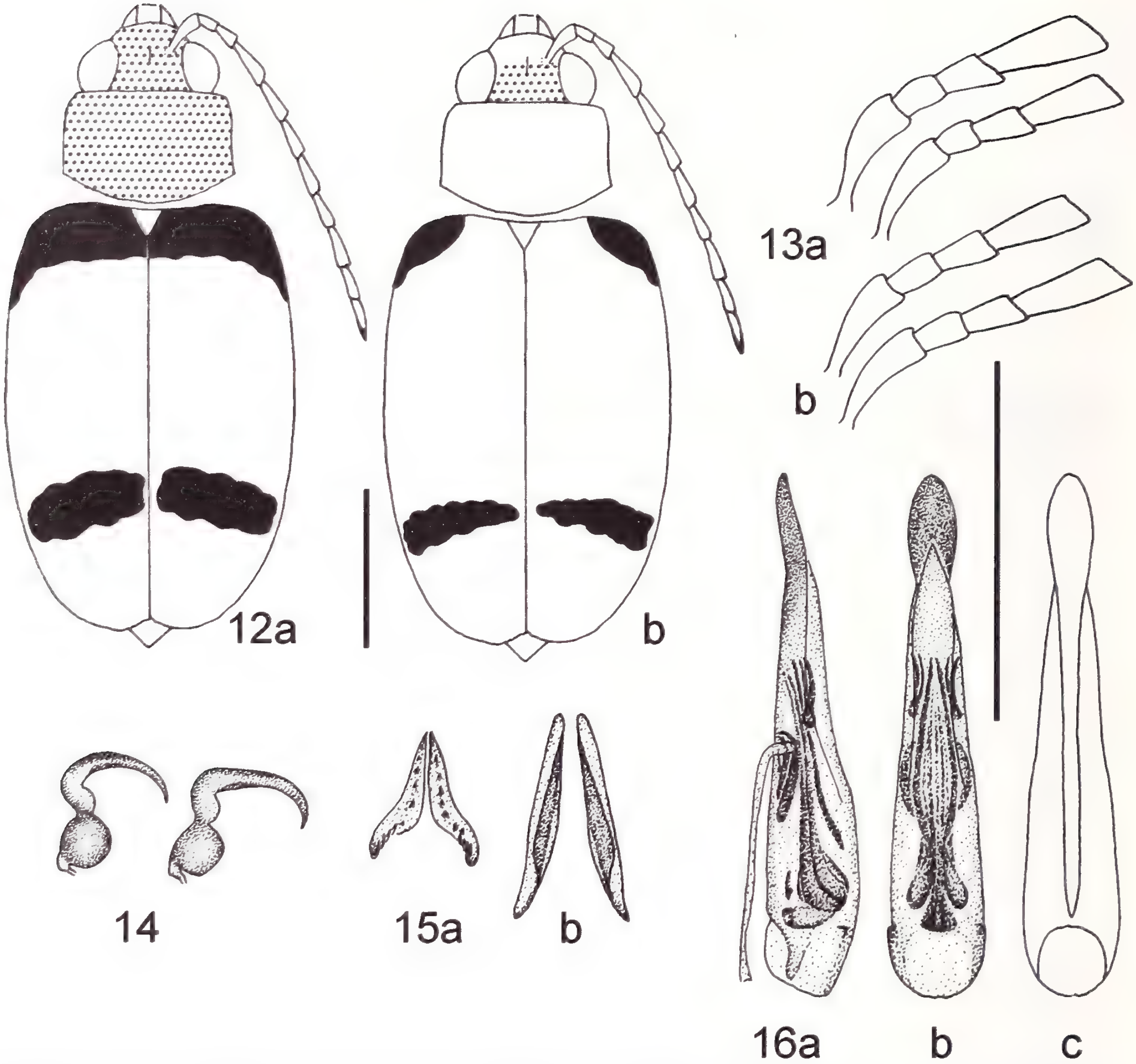
= *Monolepta sjöstedti* Weise, 1909: 212; **syn. n.**

= *Monolepta ugandaensis* Laboissière, 1920a: 52; **syn. n.**

= *Monolepta lusingensis* Laboissière, 1920b: 98; **syn. n.**

= *Monolepta bouvieri* Laboissière, 1920b: 98; **syn. n.**

= *Monolepta striola* Laboissière, 1920b: 98–99; **syn .n.**



Figs 12–16: *Monolepta lepida* Reiche, 1858 12: colour pattern; 13: basal antennal articles (a: ♂, b: ♀); 14: two different spermathecae; 15: bursa-sclerites (a: dorsal, b: ventral); 16: median lobe (a: lateral, b: dorsal, c: ventral, without endophallic structures).

= *Monolepta consociata* Laboissière, 1920b: 99; **syn. n.**

= *Monolepta rugifrons* Laboissière, 1920b: 99; **syn. n.**

= *Monolepta femoralis* Laboissière 1940b: 66; **syn. n.**

Redescription.

Total length. 3.25–4.75 mm (mean: 4.06 mm; n = 25).

Head. An entirely yellowish red to red head is typical for specimens from lowland areas of eastern and western Africa (Figs 18b, g), in montane regions of East Africa and along the Albertine Rift head often with yellow frons and black vertex (Figs 18a, d, e), frons can be also brownish (Fig. 18f) or head black throughout as in some type specimens of *M. bouvieri* and *M. sjöstedti* from Mt. Kilimandjaro, of *M. femoralis* from the Ruwenzori Mountains, and in most specimens from the Ethiopian Highlands including the type of *M. alternata* (Fig. 18c). Antennae pale yellow, only last antennomere or at most apical parts of the tenth antennomere brownish or black, antennomeres four to eleven about 4 times longer than broad at apex. Basal antennomeres comparatively short (Fig. 19), length of antennomeres two to three 0.86–1.00 (mean: 0.95), length of antennomeres three to four 0.28–0.37 (mean: 0.32).

Thorax. Prothorax pale yellow in about 60 % of specimens examined (Figs 18 a-d), others with yellowish-red to red prothorax (Figs 18e, g), very rarely prosternum black as in some types of *M. alternata* or prothorax

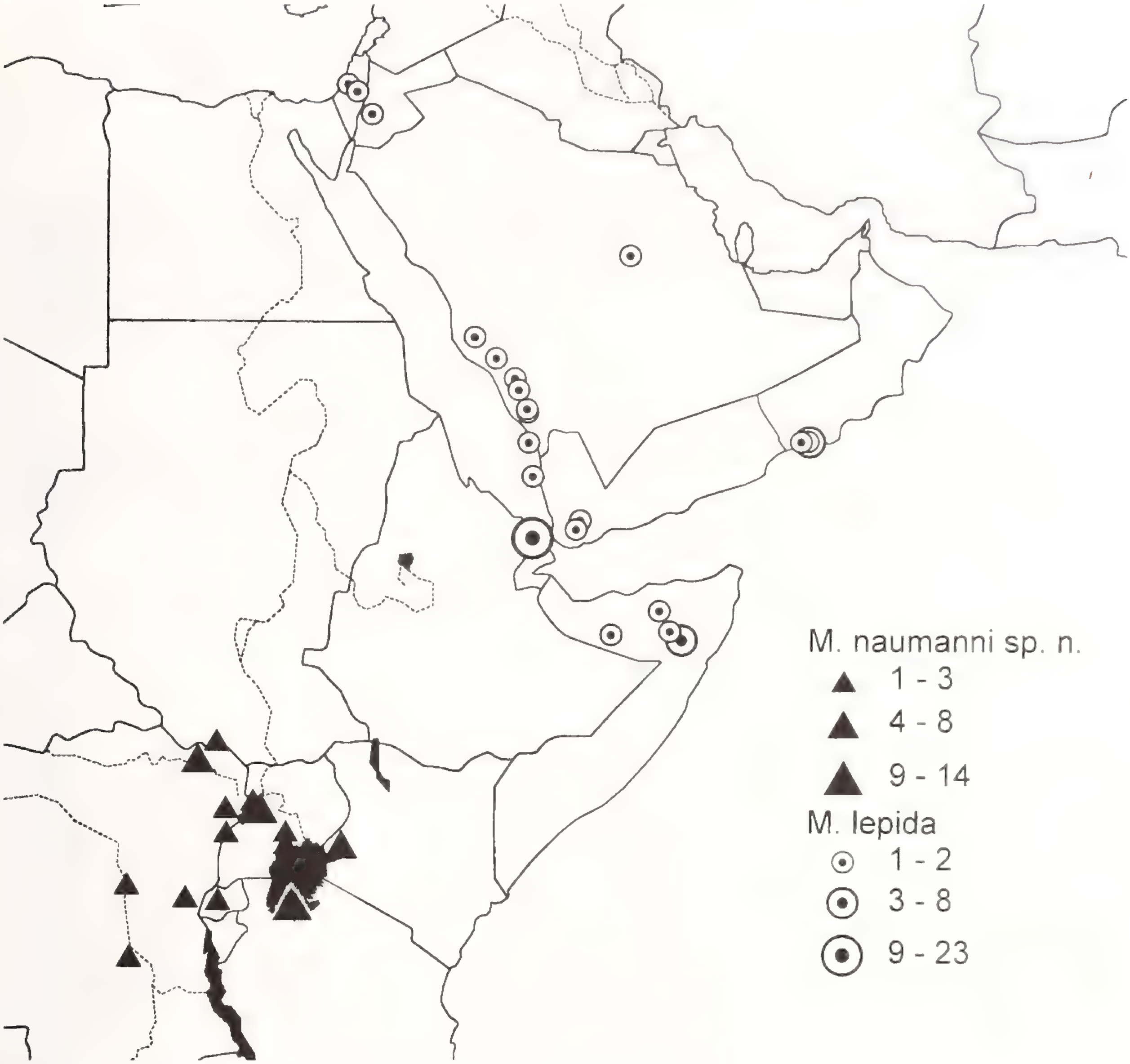
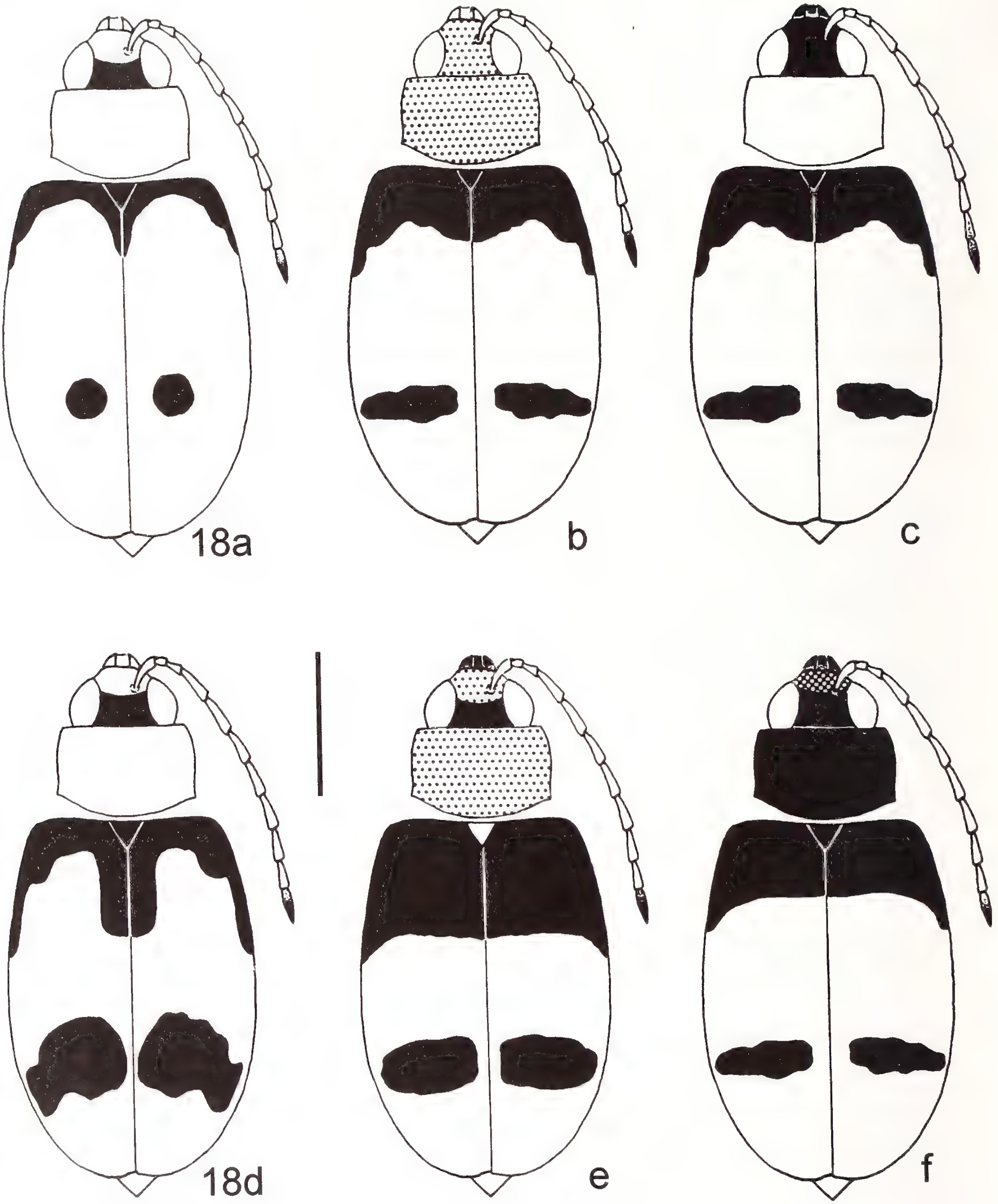
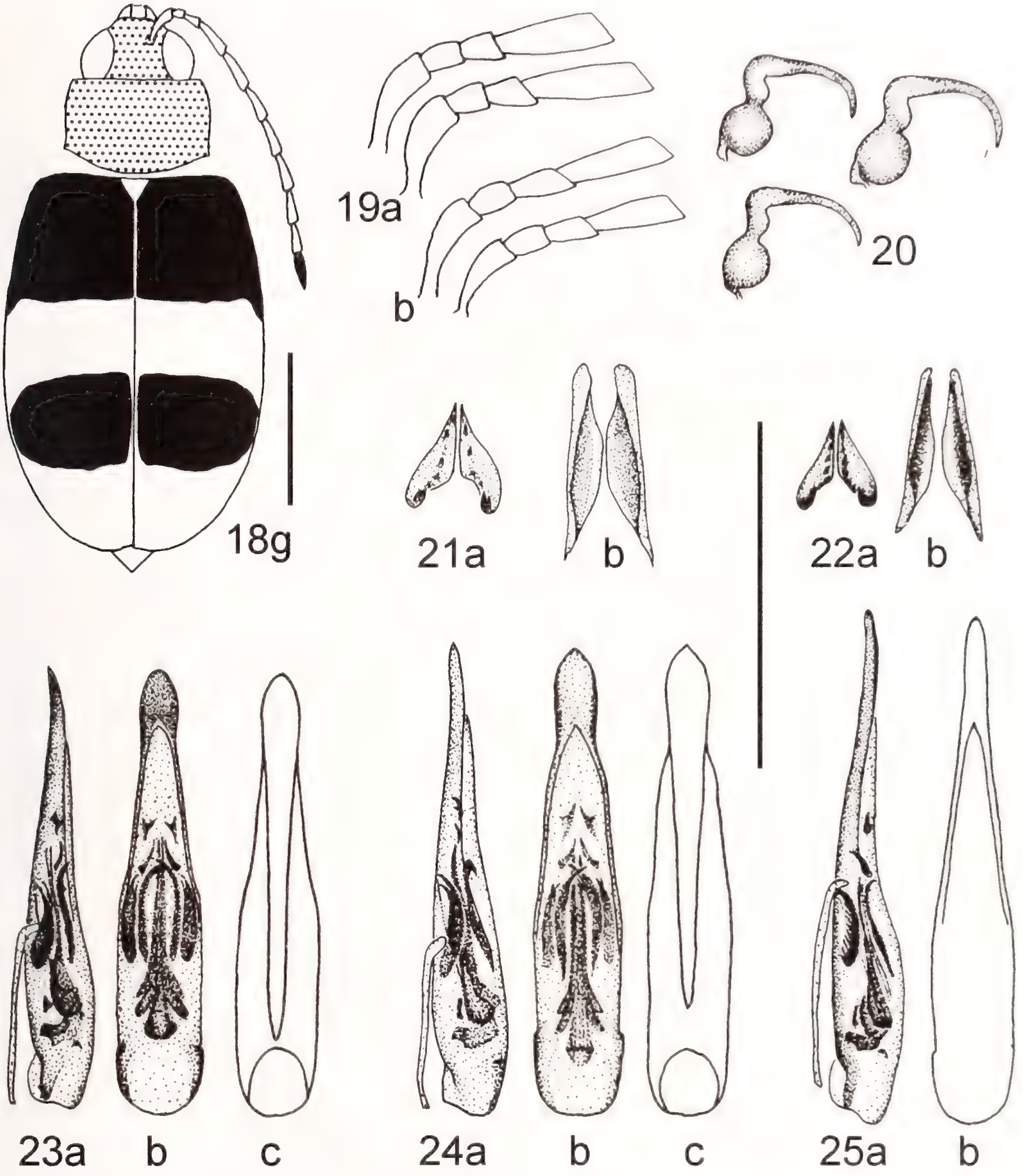


Fig. 17: Distribution of *Monolepta lepida* Reiche, 1858, and *M. naumanni* sp. n.

black throughout (Fig. 18f) as in some specimens from Uganda and Rwanda. Pronotal width 0.95–1.35 mm (mean: 1.17 mm), pronotum broad, pronotal length to width 0.58–0.64 (mean: 0.61), very finely punctured. Elytra pale yellow, to yellow, extension of black parts highly variable. Mostly reduced in specimens from montane regions of East and Central Africa, with narrow black elytral base (Fig. 18a), which is sometimes significantly extended along the outer elytral margins and the suture (Fig. 18d), subapical elytral band can be reduced to circular spots (types of *M. sjöstedti*; Fig. 18a), or subapical black spots can be extended towards the outer elytral margins (types of *M. insignis* and *M. lusingerensis*; Fig. 18d). Most specimens from mid altitude areas and lowland sites in West, Central and East Africa with more extended basal band (type of *M. vincta*; Fig. 18b, or types of *M. consociata*, *M. rugifrons* and *M. striola*; Fig. 18e). The black coloration is most extended in some specimens from the Ethiopian Highlands, and in few specimens from the Congo Basin and western Africa (Fig. 18g). Elytral length 2.50–3.60 mm (mean: 3.09 mm), maximal width of both elytra 1.70–2.35 mm (mean: 2.12 mm), maximal width of both elytra to length of elytron 0.68–0.75 (mean: 0.72). Scutellum yellow, yellowish-red or black. Meso- and metathorax, and legs usually yellowish-red, with exception of the pale yellow tibiae and tarsi. Specimens with black head from montane regions sometimes with brownish or rarely black meso- and metathorax and basal two thirds of femora can be also black, rarely un-


18a
b
c
18d
e
f



Figs 18–25: *Monolepta vincta* Gerstaecker, 1871 18: colour pattern; examples based mainly on coloration of type specimens: a: *M. sjöstedti*; b: *M. vincta*; c: *M. alternata*, *M. bouvieri*, *M. femoralis*; d: *M. insignis*, *M. lusingerensis*; e: *M. rugifrons*, *M striola*, *M. consociata*; f: rare type with black pronotum from Rwanda, Uganda; g: one coloration type from Ethiopian Highlands; 19: basal antennal articles (a: ♂, b: ♀); 20: three different spermathecae; 21: bursa-sclerites (a: dorsal, b: ventral); 22: bursa-sclerites, variation (a: dorsal, b: ventral); 23: median lobe, typical shape from Central and southern-east Africa (a: lateral, b: dorsal, c: dorsal without endophallic structures); 24: median lobe, variation, mainly Ethiopian Highlands (a: lateral, b: dorsal, c: ventral, without endophallic structures); 25: median lobe, very rare variation (a: lateral, b: dorsal, c: ventral, without endophallic structures).

derside reddish and only femora with exception of the apex black like in some types of *M. insignis*.

Abdomen. Pale yellow to yellow, in some specimens from montane regions with dark underside abdomen entirely or last sternites black.

Female genitalia. Spermatheca with spherical nodulus, slender middle part and long, slender cornu (Fig.20). Dorsal part of bursa sclerites triangular, with strongly hooked base (Figs 21a, 22a), ventral part slender, outer margin finely serrate (Figs 21b, 22b).

Male genitalia. Median lobe conical, straight, apical part nearly parallel-sided, slightly ventrally bent (Figs 23a, 24a), few specimens from the Congo Basin with very slender apical part of median lobe (Fig.25), some specimens from the Ethiopian Highlands have broader median lobes (Figs 24b, c). Tectum, pointed, ventral groove slender, slightly conical towards orifice (Figs 23b, c, 24b, c). Dorsal pair of median endophallic spiculae strong, curved or hooked at apex (Figs 23a, 24a, 25a), other median spiculae slender, long; ventral spiculae separated into two portions; two pairs of short lateral spiculae, the more basal pair slender, the more apical one triangular (Figs 23b, 24b).

Distribution. This species is widely distributed and abundant in most parts of tropical Africa, but with increasing rarity in southern Africa towards the South, and not known from the Republic of South Africa (Fig. 26).

Diagnosis. *Monolepta vincta* is most similar and very closely related to *M. melanogaster* and *M. lepida*. The latter two species are on average larger, and thus specimens smaller than 3.8 mm total length belong to *M. vincta*. However, there is a high overlap in body size. *Monolepta lepida*, which is sympatric with *M. vincta* in Somalia and Eritrea, can be distinguished by the elongated second and third antennomeres (length of second to third antennomeres: 0.75–0.88, *M. vincta*: 0.86–1.00; length of third to fourth antennomeres: 0.46–0.54, *M. vincta*: 0.27–0.35) and the narrow pronotum (pronotal length to width: 0.63–0.67, *M. vincta*: 0.57–0.64). *Monolepta melanogaster* is allopatric with *M. vincta* in South Africa and Namibia, while but both species are sympatric in Malawi, Congo, and most regions of Zimbabwe, southern Zambia, southern Moçambique and Uganda. *Monolepta vincta* can be distinguished on average by more slender elytra, shorter antennae, and by slight differences in shape of the median lobe and endophallic armature (for details see diagnosis for *M. melanogaster*). *Monolepta vincta*, *M. melanogaster*, and *M. lepida* are most likely a monophyletic group, which can be derived from external characters, coloration and male genitalic patterns. Identification of *M. lepida* and especially of *M. melanogaster* from areas where these species occur sympatrically with *M. vincta* should be confirmed by examination of the male genitalia, while females can sometimes not be allocated to species without doubt.

Other species similar to *M. vincta* are the herein described *M. sharonae* sp. n., which has the same colour pattern as the type of *M. vincta* (Fig. 18e). Both species can be clearly distinguished by examination of the male genitalia only, which are in particular different in endophallic armature (Figs 23, 24, 37). *Monolepta sharonae* sp. n. is on average smaller (total length up to 4.2 mm, *M. vincta* up to 4.7 mm), the basal antennomeres are longer (antennomere 3 to 4: 0.43–0.50, *M. vincta*: 0.28–0.37), and the transverse post antennal suture is deeply incised in all known specimens of *M. sharonae* sp. n., while this character is very rarely found in *M. vincta*. Less similar are *M. buquetii* which is also coloured like the type of *M. vincta* (Fig. 18e), but is on average smaller, has shorter antennae, and very different female and male genital characters (Figs 8, 9, 11). *Monolepta ronbeeneni* sp. n. is also much smaller than *M. vincta*, has longer antennae and more slender basal antennomeres, a more yellowish-red elytral coloration and differs also strongly in genital patterns (Fig. 31).

Discussion. Wide distribution, high abundance and high polymorphism in coloration have resulted in a high number of synonyms. After this species was first described from the coastal region in Kenya, specimens with abberative coloration, in particular from Mt. Kilimandjaro, Mt. Kenya and the Albertine Rift, were used for the description of additional species, which have turned out as synonyms. Apart from coloration, also male genital characters show some variation. Shape of the median lobe, endophallic armature, and coloration pattern varies independently and cannot be correlated to geographic distribution of single populations. It is very likely that some populations, for example some of the Ethiopian Highlands, are genetically more isolated and undergo a current speciation process. However, using morphological data only, these populations cannot be clearly distinguished from others. Molecular data might be helpful for species identity and evolutionary processes of these beetles in the future. On the base of the available morphological data, all type specimens listed are considered as conspecific with *M. vincta*.

Type material. *Monolepta vincta* Gerstaecker, 1871. Holotype: ♀ "56683 / Type / *vincta*, Gerst.*, Mombas, v. d. Deck." (ZMHB); examined (coloration like Fig. 18b); type locality: Kenya, Mombasa, 4.04S/39.40E. GERSTAECKER gave no information on the number of specimens studied, and mentioned only one locality. There is only one specimen available from this site, which is considered as holotype.

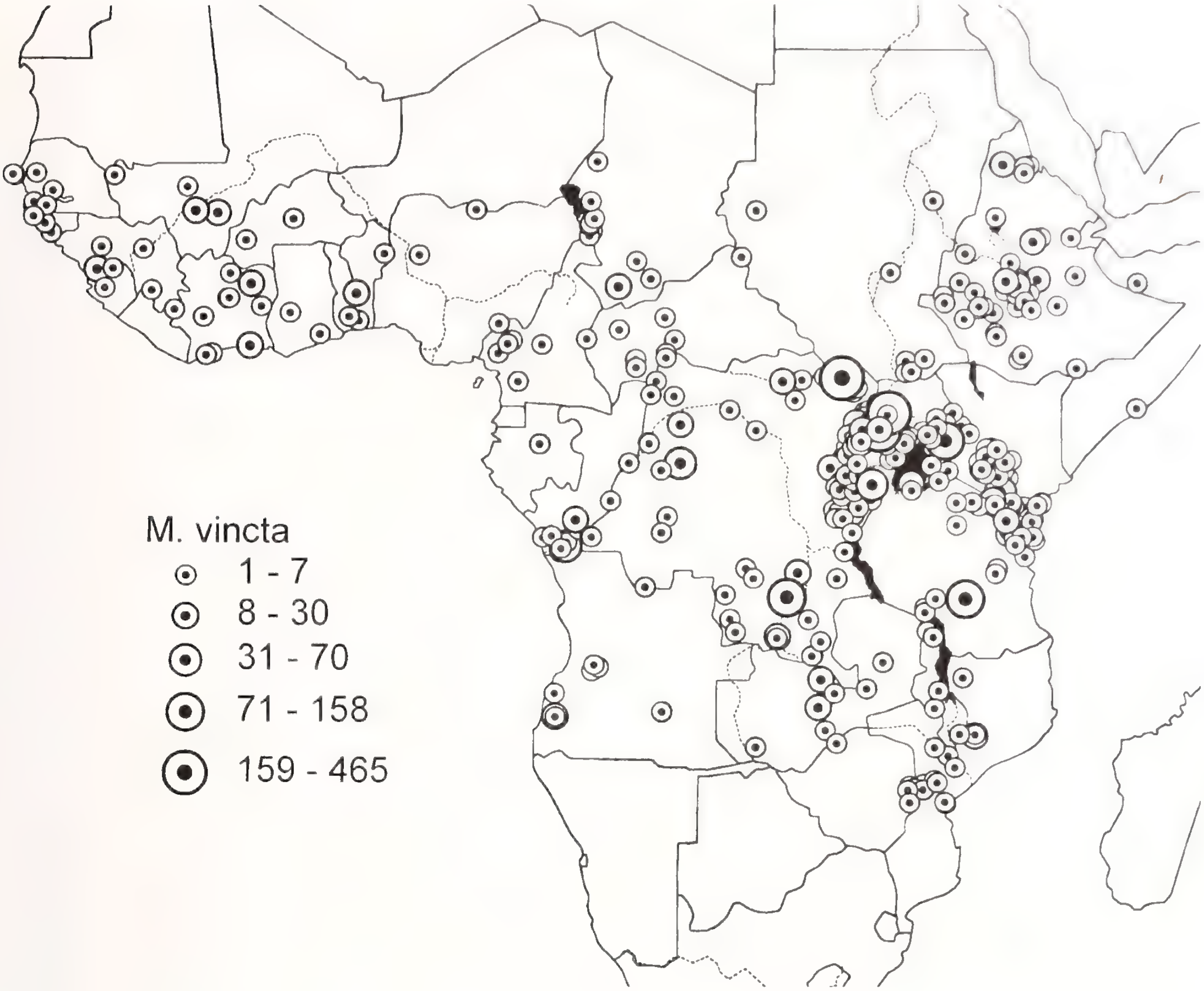


Fig. 26: Distribution of *Monolepta vincta* Gerstaecker, 1871

Monolepta alternata Chapuis, 1879. Holotype: ♀ "Abyss. Raffray / 519 / *Monolepta alternata* Chp. / Regione boschiva da Goundet ad Adoua, 1000–2000 m 1893 / Typus *Monolepta alternata* Chapuis, 1879 / Museo Civico di Genova / Holotypus *Monolepta alternata* Chapuis, 1879 / *Monolepta vincta* Gerstaecker, 1871 Th. Wagner det. 2000" (MCSN); examined (coloration like Fig. 18c); type locality: Ethiopia, province Goundet à Adoua. CHAPUIS gave no information on the number of specimens studied, and mentioned only one locality. There is only one specimen available from this site among the material in Chapuis' collection. This specimen is considered as holotype.

Monolepta insignis Weise 1903. Lectotype: ♂ "Mombo 7.99 / ex. coll. J. Weise / Type / *Monolepta insignis* m. / Lectotypus *Monolepta insignis* Weise, 1903 Th. Wagner desig. 2003 / *Monolepta vincta* Gerstaecker, 1871 Th. Wagner det. 2003" (ZMHB); this designation; examined (coloration like Figs 18a, d); type locality: Tanzania, Mombo, 4.54S/38.18E. – Paralectotypes: 12 ex. "Mombo" or "Mombo 7.99 / ex. coll. J. Weise", 6 ex. additionally "Type", 1 ex. additionally "*Monolepta insignis* m." (ZMHB); 2 ex. same data (NHRS).

Monolepta sjöstedti Weise, 1909. Lectotype: "Kilimandj. *Sjöstedt* / Kibonoto, Kulturz[one] / Type / Typus / 18. Dec./ sjöstedti m / Lectotypus *Monolepta sjöstedti* Weise, 1909 Th. Wagner desig. 2003 / *Monolepta vincta* Gerstaecker, 1871 Th. Wagner det. 2003" (NHRS); this designation; examined (coloration like Figs 18a, b, d); type locality: Tanzania, Mt. Kilimandjaro, 3.04S/37.22E. – Paralectotypes: 1 ex. "Meru Regenwald / Meru Sjöstedt" (NHRS); 6 ex. "Kilimandjaro Sjöstedt" including 4 ex. additionally "Kibonoto, Kulturz[one]" including 1 ex. "Type", 2 ex. additionally "Kibonoto Nieder[ung]" (NHRS), the paralectotypes bear additional labels indicating day and month of collection. Weise mentioned eight specimens from three locations in his original publication, which could be all located in NHRS.

Monolepta ugandaensis Laboissière, 1920a. Holotype: ♂ "Museum Paris Ouganda Ounyoro Méridional Ch. Alluaud 1909 / Janvier / *Monolepta ougandensis* [sic!] m. V. Laboissière – Dét. 1919 / Holotypus / *Monolepta vincta* Gerstaecker, 1871 Th. Wagner det. 2003". (MNHN), examined (coloration type as Fig. 18g). Laboissière cited only data of one specimen "Muséum de Paris", holotype by monotypy after article 73.1.2, ICZN rules.

Monolepta lusingensis Laboissière, 1920b. Lectotype: ♂ "Oct. / Museum Paris, Afrique Orient. Angl., Ile de Lusinga, Victoria-Nyanza, N.-E. Ch. Alluaud 1904 / Type / *Monolepta lusingensis* m. V. Laboissière – Det. / Lectotypus *Monolepta lusingensis* Laboissière, 1920 Th. Wagner desig. 2003 / *Monolepta vincta* Gerstaecker, 1871 Th. Wagner det. 2003" (MNHN); this designation; type locality: Lusinga Island, location? – Paralectotypes: 1 ♀ same data as lectotype (MNHN); 1 ♀ "Museum Paris, Afrique Orient. Angl., Ile de Lusinga, Victoria-Nyanza, N. E., Ch. Alluaud 1904 / Oct. / Type / *Monolepta lusinga*[sic!]*ensis*" (ZMUH); examined (coloration type as Fig. 18d). Laboissière mentioned at least two specimens "Muséum Paris et coll. Laboissière" from one locality in his original publication.

Monolepta bouvieri Laboissière, 1920b. Holotype: ♀ "Museum Paris, Afrique Orient. All., Kilimandjaro, Zone des Forêts, Kiboscho, 1700 m, Ch. Alluaud 1904 / mars / Type / *Monolepta bouvieri* Laboi. V. Laboissière – Det. / Holotypus / *Monolepta vincta* Gerstaecker, 1871 Th. Wagner det. 2000" (MNHN); examined (coloration similar to Fig. 18d); type locality: Tanzania, Mt. Kilimandjaro, 3.04S/37.22E. Laboissière mentioned "un individu, Muséum de Paris", holotype by monotypy after article 73.1.2, ICZN rules.

Monolepta striola Laboissière, 1920b. Lectotype: ♀ "Museum Paris, Ouganda Central, Ch. Alluaud 1909 / décembre / Type / *Monolepta striola* Laboi. V. Laboissière – Det. / Lectotypus *Monolepta striola* Laboissière, 1920 Th. Wagner desig. 2003 / *Monolepta vincta* Gerstaecker, 1871 Th. Wagner det. 2003" (MNHN); this designation; examined (coloration similar to Fig. 18e); type locality: Central Uganda. – Paralectotype: 1 ♂, same data as lectotype. Laboissière mentioned at least two specimens "Muséum Paris et coll. Laboissière" from one locality in his original publication.

Monolepta consociata Laboissière, 1920b. Holotype: ♂, "Afrique or. Anglaise, Mt. Kénya vers ouest, Zone inférieure, Alluaud & Jeannel / Riviére Amboni, Vallée boisée, 1800m, Janv.-Fév. 1912- St. Et 51 / Type / Museum Paris, coll. Générale / *Monolepta consociata* Lab. V. Laboissière – Det. / Holotypus / *Monolepta vincta* Gerstaecker, 1871 Th. Wagner det. 2003" (MNHN); examined (coloration like Fig. 18e); type locality: Kenya, Mt. Kenya, 0.09S/37.19E. Laboissière mentioned "un exemplaire, Muséum de Paris", holotype by monotypy after article 73.1.2, ICZN rules.

Monolepta rugifrons Laboissière, 1920b. Holotype: ♂ "Museum Paris, Afrique Orient. Angl., Kénia N.-O., Prairies 2000 m, Ch. Alluaud 1909 / novembre / Type / *Monolepta rugifrons* Laboi. V. Laboissière – Det. / Holotypus / *Monolepta vincta* Gerstaecker, 1871 Th. Wagner det. 2003" (MNHN); examined (coloration like Fig.18e); type locality: Kenya, Mt. Kenya, 0.09S/37.19E. Laboissière mentioned "un ♂, Muséum de Paris", holotype by monotypy after article 73.1.2, ICZN rules.

Monolepta femoralis Laboissière 1940. Lectotype: ♀ "Holotype *femoralis* [invalid indication] / Congo Belge: P.N.A., Rwindi, 1000m, 22. au 24.-xi-1934, G. F. de Witte: 792 / Lectotypus Monolepta femoralis Laboissière, 1940 Th. Wagner desig. 2003 / *Monolepta vincta* Gerstaecker, 1871 Th. Wagner det. 2003" (MRAC); this designation; examined (coloration like Fig. 18c); type locality: Congo, Kivu, Rwindi, 0.47S/29.17E. – Paralectotypes: 7 ex. "Paratype *femoralis*" / Congo Belge: P.N.A., Rwindi, 1000m, 22. au 24.-xi-1934, G. F. de Witte: [several numbers]" (1 ex. IRSNB, 6 ex. MRAC); 3 ex. "Paratype *femoralis*" / Congo Belge: P.N.A., Ndeko (Près Rwindi), 1082m, 27-xi-1934, G. F. de Witte: 839" (MRAC); 1 ex. "Paratype *femoralis*" / Congo Belge: P.N.A., Entre Kalinga et Bitshumbi, 1082m–925m, 12–xi–1934, G. F. de Witte: 741" (MRAC). Laboissière mentioned 17 specimens from the four locations in his original publication of which were 12 specimens available.

Further material examined. Angola: 1 ex., Dundo, 12.35S/15.12E, VIII.1953, E. Luna de Carvalho (MRAC); 1 ex., 5 mls SW Cacula, 12.22S/15.34E, III.1972, Southern African Exp. B.M. 1972–1, at light (BMNH); 8 ex., Salazar, 9.18S/14.55E, III.1972, Southern African Exp. B.M. 1972–1, at light (BMNH); 3 ex., Bruco, 15.07S/13.11E, III.1972, Southern African Exp. B.M. 1972–1, damp leaf litter by stream (BMNH); 1 ex., 12 mls SW Luimbale, 12.15S/15.19E, III.1972, Southern African Exp. B.M. 1972–1, at light (BMNH); 1 ex., Dolondola, 13.49S/13.07E, XI.1974 (NMNW). – **Benin:** 1 ex., Niaouli, mais station, 6.45N/2.08E, VI.1952 (MNHN); 3 ex., Zanbbara, 10.28N/3.32E, IX.1969, G. Pierrard (MRAC). – **Burkina Faso:** 1 ex., Bobo-Dioulasso, 11.11N/4.08W, X.1964, R. Siffointe (MRAC); 4 ex., Quagadougou, 12.22N/1.31W, XI.1973, R. Linnavuori (MZHF). – **Burundi:** 2 ex., Bururi, 3.48S/29.35E, ex coll. Breuning (MRAC); 1 ex., Urundi, II.1897, Ramsay & Hösemann (ZMHB); 1 ex., Mahembe, terr. Nyanza, 1400 m, I.1953, P. Basilewsky (MRAC); 1 ex., Bururi, II.1959, P. Giraudin (MNHN); 2 ex., Mugera, 3.04S/30.40E, 1965, J. J. Rwabuneza (MRAC); 6 ex., Bururi, 1800–2000 , III.1953, P. Basilewsky (3 BMNH, 3 MRAC); 1 ex., Bujumbura, 3.22S/29.31E, IX.1969, P. Giraudin, ex coll. Breuning (MRAC); 2 ex., Ngozi, 2.52S/29.56E, II.1979,

J. Decelle (MRAC); 3 ex., Gitega, 3.29S/29.57E, II.1979, J. Decelle (MRAC). – **Cameroon:** 2 ex., Kamerun, Tessmann (ZMHB); 2 ex., Victoria, 4.02S/9.21E (MNHN, HNHM); 1 ex., Joko, 5.29N/12.19E (ZMHB); 1 ex., Ndzida Forest, V.1952 (MNHN); 1 ex., Joko, I.1957, J. Cantaloube (MRAC); 3 ex., N'Kongsamba, 4.59N/9.53E, V.1957, J. Cantaloube (MNHN); 2 ex., Bas Logone, Birni, 11.47N/15.05E, VIII.1963, J. Péricart (MNHN); 1 ex., N'Kolbisson, 3.25N/11.00E, VI.1966, B. de Miré (MNHN); 1 ex., Plateau de Kounden, 5.42N/10.40E, VIII.1967, L. Matile (MNHN); 1 ex., Haute Nguemba, VIII.1967, L. Matile (MNHN); 1 ex., Bafoussam, 5.31N/10.25E, II.1969, N. Berti (MNHN); 5 ex., Logone-Ufer, 65 km S. F. Foureau, 11.30N/14.56E, VII.1978, *Salix* (CMa). – **Central African Republic:** 1 ex., Pays Mandjia, 5.46N/19.43E, Miss. Chari-Tchad, 1904, J. Decourse (MNHN); 1 ex., Bessou, amont Fort de Possel, 4.41N/17.33E, Miss. Chari-Tchad, VI.1904, J. Decourse (MNHN); 2 ex., Fort de Possel, 5.01N/19.15E, Miss. Chari-Tchad, IX.1904, J. Decourse (MNHN); 2 ex., Babua, Obersanga, 5.48N/14.49E, II.1914, Tessmann (ZMHB); 6 ex., Bosum, Uam-Gebiet, 6.19N/16.38E, III.1914, Tessmann (ZMHB); 2 ex., Bambari, 4.13N/17.35E, III.1964, G. Pierrad (MRAC). – **Chad:** 5 ex., Gory-Damraou, 10.06N/17.35E, Miss. Chari-Tchad, VI.1904, J. Decourse (MNHN); 3 ex., Fort Archambault, 9.08N/18.22E, Bahr el Azreg, Miss. Chari-Tchad, V.1904, J. Decorse (MNHN); 1 ex., N'Gouri, Kanem distr., 15.38N/15.22E, VIII.1958, P. Renaud (MRAC); 1 ex., Bas Chari, env. de Fort Foureau, 12.05N/14.56E, VII.1963, J. Péricart (MHNH); 1 ex., Bas Chari, env. de Fort Lamy, Farcha, 12.10N/14.59E, VII.1967, J. Péricart (MNHN); 9 ex., Bebedja, 8.41N/16.34E, V.1973, R. Linnavuori (MZHF); 1 ex., Farcha, 12.27N/15.13E, V.1973, R. Linnavuori (MZHF); 1 ex., Lamto, 13.24N/15.01E, V.1990, H. Perrin (MNHN). – **Congo-Brazzaville:** 2 ex., Fort-Crampel, 7.00N/19.10E (ZMUH). – **Congo:** 1 ex. (NHRS); 1 ex., Dybowski (MNHN); 1 ex. Tavares (ZMHB); 3 ex., Chiloango, 5.12S/12.07E, Tschoffen (2 ex. IRSNB, 1 ex. MRAC); 3 ex., Matadi, 5.59S/13.27E Tschoffen (IRSNB); 1 ex., Ituri, La Moto, Madyu, 2.54N/29.37E, L. Burgeon (MRAC); 7 ex., Banana Boma, 6.01S/12.24E, 1891, M. Tschoffen, Jacoby coll., *pulchella* Klug (1 ex. BMNH, 4 ex. IRSNB, 2 ex. MRAC); 1 ex., SW Albert-Njansa, Undussuma, 1050 m, VII.1891, Stuhlmann (ZMHB); 1 ex., SW Albert-Njansa, Buessa, VIII.1891, Stuhlmann (ZMHB); 4 ex., Dima, 3.29N/18.42E, IX.1908, A. Koller (MRAC); 1 ex., Matadi, , IX.1910, Dr. Bequaert (MRAC); 45 ex., Congo da Lemba, 5.42S/13.42E, V., X.–XII.1911, V., X.1912, I.–III.1913, R. Mayné (MRAC); 4 ex., Elisabethville, 11.40S/27.28E, X.1911, Miss. Agric. (MRAC); 3 ex., Kapiri, 9.42S/27.13E, X.1912, Miss. Agric. (MRAC); 1 ex., Banza, Manteka, 5.28S/13.47E, VI.1912, R. Mayné (MRAC); 2 ex., Amadi, 3.35N/26.47E, II.1913, P. van den Plas (MRAC); 1 ex., Kiniati-Zobe, 5.07S/12.37E, XII.1915, R. Mayné (MRAC); 1 ex., Mayumba, Zobe, 5.07S/12.37E, I.1916, R. Mayné (MRAC); 2 ex., Mayumbe, Lemba, 4.45S/14.15E, VII.1917, R. Mayné (MRAC); 8 ex., Nyangwe, 4.13S/26.11E, III.–IV.1918, R. Mayné (MRAC); 1 ex., Albertville, 5.56S/29.12E, XII.1918, R. Mayné (MRAC); 1 ex., Madyu, 1919, L. Burgeon (MNHN); 1 ex., Kisantu, 5.07S/15.05E, V,1919, P. Vanderijst (MRAC); 1 ex., Boma, VII.1920, H. Schouteden (MRAC); 3 ex., Haut-Uele, Watsa, 3.03N/29.32E, XI.1919, 1922, L. Burgeon (MRAC); 1 ex., Dungu, 3.37S/28.34E, IV.1920, P. van den Plas (MRAC); 2 ex., Matadi, 5.49S/13.27E, X.1920, L. Burgeon (MRAC); 2 ex., Elisabethville, R. Lubumbashi, XI.1920, M. Bequaert (MRAC); 4 ex., Haut-Uele, Moto, 2.27N/26.25E, 1922, 1923, I.1925, L. Burgeon (MRAC); 1 ex., Kwamouth, 3.10S/16.12E, I.1922, H. Schouteden (MRAC); 5 ex., Haut-Uele, Abimva, 3.09N/29.50E, V.-VII.1925, L. Burgeon (MRAC); 1 ex., Katanga, Nyonga, V.1925, G. F. de Witte (MRAC); 4 ex., Haut-Uele, Yebo Moto, I.-II., IX.1926, L. Burgeon (MRAC); 1 ex., Kivu, Mokoto, 1.15S/29.00E, 1927, G. Babault (MNHN); 2 ex., 18 m SW of Elisabethville, 11.42S/27.25E, 1927, Dr. H. S. Evans (BMNH); 2 ex., alto Uelle, fl. Duru 3.45N/28.02E, III.1927, F. S. Pratizi (MCSN); 3 ex., alto Uelle Yakuluku, 4.20N/28.48E, IV.1927, F. S. Patrizi (MCSN); 1 ex. alto Uelle, Kapili, 3.42S/27.53E, V.1927, F. S. Patrizi (MCSN); 1 ex., Uvira, 3.24S/29.08E, 1930, G. Babault (MNHN); 1 ex., Lomami, Kambaye, 6.53S/23.44, VIII.1930, P. Quarré (MRAC); 1 ex., Lulua, Sandoa, 9.41S/22.52E, X.1930, G. F. Overlaet (MRAC); 18 ex., Kivu, Rwindi, 0.47S/29.17E, 1000 m, XI.1931, XI.1934, G. F. de Witte (IRSNB); 1 ex., Ubangi, Dongo, 2.43N/18.24E, XII.1931, H. J. Brédo (MRAC); 1 ex., Lulua, Tshala, 7.56S/18.08E, VII.1932, G. F. Overlaet (MRAC); 3 ex., Lomami, Kaniama, 00.46N/24.16E, VII.1932, R. Massart (MRAC); 1 ex., Ruwenzori, Kalonge, 0.20N/29.48E, 2050 m, VIII.1932, L. Burgeon (MRAC); 1 ex., Beni, 0.30N/29.28E, VIII.1932, L. Burgeon (MRAC); 1 ex., Kivu, Lulenga, 1.25S/29.23E, IX.1932, L. Burgeon (MRAC); 3 ex., Kivu, Ngoma, 2.04S/29.55E, X.1932, L. Burgeon (MRAC); 1 ex., Kivu, Katana, XI.1932, L. Burgeon (MRAC); 3 ex., Lulua, Kapanga, 8.21S/22.35E, XII.1932, III.1933, F. G. Overlaet (MRAC); 1 ex., Luvungi, 2.52S/29.02E, XII.1932, L. Burgeon (MRAC); 1 ex., Albertville, I.1933, l. Burgeon (MRAC); 38 ex., Kivu, Rutshuru, 1.11S/29.27E, 1285 m, XII.1933, VI.1934, VI.-VII.1935, G. F. de Witte (25 ex. IRSNB, 12 ex. MRAC); 3 ex., Kilo, Dele, 1.49N/30.16E, IV.1934, H. J. Brédo (MRAC); 2 ex., Ruhengeri, Source Kirii, 1.27S/19.00E, 1800 m, X.1934, G. F. de Witte (IRSNB, MRAC); 24 ex., P.N. Albert, Ndeko, 1.04N/20.04E, 1082 m, XI.1934, G. F. de Witte (12 ex. IRSNB, 12 ex. MRAC); 4 ex., P.N. Albert, May ya Moto, 0.53S/29.21E, 950 m, XI.1934, G. F. de Witte (IRSNB); 2 ex., P.N. Albert, Camp Rwindi, 0.48S/29.18E, 1000 m, XI.1934, G. F. de Witte (MRAC); 2 ex., P.N. Albert, Escarpment de Kabasha, 0.45S/29.13E, 1500 m, XII.1934, G. F. de Witte (IRSNB); 2 ex., Bunia, 1.34N/30.15E, IV.1935, H. J. Brédo (MRAC); 4 ex., P.N. Albert, Nyasheke, Volc. Nyamuragira, 1.23S/29.19E, 1820 m, VI.1935, G. F. de Witte (IRSNB); 2 ex., P.N. Albert, Mayumbu, Volc. Nyamuragira, 1.25S/29.12E, 2100 m, VI.1935, G. F. de Witte (IRSNB); 2 ex., P.N. Albert, R. Ondo, affl. Rutshuru, VII.1935, H. Damas (MRAC); 3 ex., Kasenyi, 7.26S/24.10E, VII., IX.1935, VIII.1937, H. J. Brédo (MRAC); 3 ex., Eala, 0.04N/18.17E, IV.1936, J. Ghesquière (MRAC); 1 ex., P.N. Albert, Bitshumbi, 0.39S/29.22E, IV.1936, L. Lippens (IRSNB); 10 ex., P.N. Albert, r. Rwindi, II.–IV.1936, L. Lippens (MRAC); 61 ex., Rutshuru, V.1936, I.–V.1937, L. Lippens / Ghesquière (MRAC); 21 ex., Bambesa, 3.28N/25.43E, V.1937, J. Vrijdagh (IRSNB); 1 ex., Djugu, 1.55N/30.30E, V.1937, H. J. Brédo (MRAC); 11 ex., Nioka, 7.07S/26.37E,VII.1937, H. J. Brédo / J. Ghesquière (MRAC); 3 ex., Ituri, Bunia, 1.34N/30.15E, VII.1937, H. J. Brédo (1 ex. IRSNB, 2 ex. MRAC); 1 ex, Lac Albert, Mahagi, 2.18N/30.59E, VII.1937, J. Ghesquière (MRAC); 3 ex., Logo, 2.11N/30.56E, VII.1937, H. J. Brédo (MRAC); 1 ex., Lukolela, 1.03S/17.12E, 1938, R. Massart (IRSNB); 1 ex., Ubangi, Budjala, 2.39N/19.42E, VII.1938, C. Léontovitch (MRAC); 1 ex., Elisabethville, I.1939, H. J. Brédo (IRSNB); 1 ex., Mulungu, 4.54S/19.02E, 1939, Hendrickx (MRAC); 1 ex., Mayidi, 5.11S/15.09E, 1912, P. van Eyen (MRAC); 1 ex., Terr. Tanganika, Malonge, 10.24S/23.10E, VI.1943, H. J. Brédo (IRSNB); 1 ex., Terr. Tanganika, Katete, 10.54S/27.54E, VII.1943, H. J. Brédo (IRSNB); 1 ex., P.N. Albert, Kiseguro, riv. Mwindi, IV.1945, G. F. de Witte (MRAC); 3 ex., P.N. Albert, Rumangabo, 1.20S/29.22E, IV.1945, G. F. de Witte (MRAC); 158 ex., P.N. Upemba, 8.30S/26.00E, several locations, VI.1945, III., X., XII.1947, II.–VII., X.1948, I.1949, G. F. de Witte (2 ex. IRSNB, 48 ex. MRAC); 3 ex., W. Ruwenzori, 0.23N/29.54E, 6000 ft., VII.1945, v. Someren (NMK); 10 ex., Rwankwi, 1.32S/29.32E, IV.1946, IV.1948, XII.1947, VI., XI.1951, J. V. Leroy (MRAC); 1 ex., Bukima, IV.1948, J. V. Leroy (MRAC); 1 ex., Stanleyville, Yaolema, 1.54N/22.47E, IV.1949, R. Laurent (MRAC); 1 ex., P.N. Upemba, Lusinga, 8.56S/27.12E, 1760 m, V.1949, G. F. de Witte (IRSNB); 465 ex, P.N. Garamba, 3.40N/29.00E, several sub locations, XII.1949, I.–III., V.,VIII., X.–XI.1950, I.–XII.1951, I.–III., VI.–VII.1952, Miss. H. de Saeger (65 ex. IRSNB, 400 ex. MRAC); 19 ex., Elisabethville, XI.1950/VI.1951, 1953, 1955, I.1956, I.1957, IX.1958, V.1959, Ch. Seydel (MRAC); 4 ex., P.N. Albert, Bomboka, Kyandolire, 1650 m, X.1952, P. Vanschuytbroeck & J. Kekenbosch (MRAC); 1 ex., Tanganika, Kamena, 7.25S/28.46E, 1400 m, Riv. Kinga, I.1953, H. Bomans (MRAC); 10 ex., P.N. Albert, Kalonge, 1.18S/28.24E, 2060 m, II.1953, P. Vanschuytbroeck & J. Kekenbosch (MRAC); 2 ex., P.N. Albert, Haut Lume, Nyamgaleka, 0.15N/29.48E, 2120 m, IV.1953, P. Vanschuytbroeck & J. Kekenbosch (MRAC); 1 ex., P.N. Albert, Moyenne Lume, Kiribata, 0.16N/29.48E, 1760 m, IV.1953, P. Vanschuytbroeck & J. Kekenbosch (MRAC); 1 ex., P.N. Albert, Migeri, riv. Kamukungu, 1700 m, IV.1953, P. Vanschuytbroeck & J. Kekenbosch (MRAC); 2 ex., Lubero, Mulo, 0.08S/29.16E, 1950 m, II.1954, R. R. P. P. Celis-Bergmans (MRAC); 1 ex., Tanganika, Albertville, IV.–V.1955, H. Bomans (MRAC); 1 ex., Uvira, Itombwe, Hte. Kambekulu, 4.04S/28.40E, 2450 m, VI.1955, N. Leleup (MRAC); 1 ex., P.N. Albert, Mt. Musima, 2.19S/29.17E, 2450 m, IV.1955, P. Vanschuytbroeck & R. Fonteyn (MRAC); 2 ex., P.N. Albert, Tschiaberimu, Mt. Buliwa, 2.04S/28.55E, 2450 m, IV.1955, P. Vanschuytbroeck & R. Fonteyn (MRAC); 14 ex., P.N. Albert, Mt. Hoyo, 1.13N/29.49E, 1280 m, VII.1955, P. Vanschuytbroeck (3 ex. IRSNB, 11 ex. MRAC); 1 ex., Kivu, Luvungi, 2.52S/29.02E, III.1956, J. Decelle (MRAC); 1 ex., P.N. Albert, Kanyatsi, 0.35S/29.18E, 912 m, VII.1956, P. Vanschuytbroeck & J. Kekenbosch (MRAC); 1 ex., P.N. Albert, Kasindi-Port, 2.20S/28.42E, 912 m, VII.1956, P. Vanschuytbroeck (MRAC); 1 ex., P.N. Albert, Semliki, 0.08S/29.36E, 912 m, VIII.1956, P. Vanschuytbroeck (MRAC); 1 ex., P.N. Albert, Molidi, Watalinga, 0.40N/29.40E, 1210 m, IX.1956, P. Vanschuytbroeck (MRAC); 1 ex., P.N. Albert, Rugetsi, 0.13N/29.40E, 1100 m, X.1956, P. Vanschuytbroeck (MRAC); 2 ex., P.N. Albert, Ihumbia, 0.00/29.40E, 1050 m, XI.1956, VIII.1957, P. Vanschuytbroeck (MRAC); 1 ex., P.N. Albert, Téte de source Indray, 1840 m, XI.1956, P. Vanschuytbroeck (MRAC); 2 ex., P.N. Albert, Mati, Talya, 0.31N/29.20E, 1180 m, I., VIII.1957, P. Vanschuytbroeck (MRAC); 1 ex., P.N. Albert, Mutsora, 0.19N/29.45E, 1340 m, II.1957, P. Vanschuytbroeck (MRAC); 1 ex., P.N. Albert, Kanyatsi, Lac Edourd, 0.08S/29.37E, 912 m, V.1957, P. Vanschuytbroeck (MRAC); 1 ex., M'Paka, terr. Libenge, 4.46N/19.14E, VII.–VIII.1959, M. Pecheur (MRAC); 9 ex., Lualaba, Ruwe, 10.39S/25.30E, II.1960, V. Allard (MRAC); 2 ex., Katanga, Kolwezi, 10.43S/25.28E, X.1961, V. Allard (MRAC); 1 ex., Mongo, 0.02N/18.19E, III.1975 (MZUF); 1 ex., Baraka, 4.06S/29.06E, VIII.1979, coll. Roggeman (CBe). – **Eritrea:** 1 ex., Erythrée, coll. Clavareau (MRAC); 2 ex., Asmara, 15.20N/38.56E (BMNH, MNHN); 2 ex., Dint. Di Massaua, 15.30N/39.20E, 1884, Frasca (MCSN); 13 ex., Agordat, 15.33N/37.53E, I.1906, D. Figini (MCSN); 10 ex., Agordat, II.1930, E. Zavattari (MCSN); 3 ex., Ghinda, 15.27N/39.03E, III.1906, D. Figini (MCSN); 1 ex., Decamere, 15.04N/39.03E, V.1963, R. Linnavuori (MZHF). – **Ethiopia:** 1 ex., Abyssinie, coll. Clavareau (MRAC); 3 ex., Abyss., Raffray, ex Mus. E. Allard (MNHN); 10 ex., Abyssinia, Vallis Erer, 9.10N/39.50E, Kovács (HNHM); 1 ex., N. Dalla, 7.43N/40.55E, Jando (MNHN); 6 ex., Tigre, 1850, Schimper (MNHN); 1 ex., Abyssinie, Voy. A. Raffray, 1881 (MNHN); 1 ex., Arussi Galla, Ganale Gudda, 4.16N/42.01E, V.1893, V. Bottego (MCSN); 2 ex., Kashinuaha, Tshertsher, I.1899, Dmitriev (ZISP); 1 ex., Buroma, Tshertsher, I.1899, Dmitriev (ZISP); 1 ex., N. Galla, 11.30N/40.00E, XI.1900, v. Erlanger (ZMHB); 1 ex., Wallega, 9.00N/35.30E, VI.1904, Dmitriev (ZISP); 3 ex., Addis Abeba, 9.02N/38.42E, XII.1910, C. Citerni (MCSN); 3 ex., Between Addis Allem and Djem Djem, 9.02N/38.24E, 7000–8000 ft, IX.1926, H. Scott (BMNH); 1 ex., Plains NW of lake Zwai, 7.56N/38.43E, 5500–6000 ft, X.–XI.1926, H. Scott (BMNH); 5 ex., Mt. Chillálo, 7.55N/39.16E, 8500 ft, XI.1926, H. Scott (BMNH); 1 ex., Mt. Chillálo, 7000–8000 ft, XI.1926, J. O. Cooper (BMNH); 5 ex., Addis Abeba, 1928, 1930, Schürhoff (ZMHB); 1 ex., Gondar, 12.36N/37.28E, 1932, Miss. M. Griaule (MNHN); 1 ex., Arero, 4.45N/38.49E, IV.1937, Miss. Zavattari nei Borana (Trieste); 1 ex., El Diee, V.1939, Miss. Zavattari Sagan Omo (Trieste); 1 ex., Caschei nei Borana, 5.00N/39.00E, VII.1939, Miss. Zavattari (Trieste); 1 ex., V. Zuai, 8.00N/38.50E, II.1954, Exped. Smeds (MZHF); 2 ex., Asella, 7.57N/39.08E, VIII.1954, Exped. Smeds (MZHF); 2 ex., Belleta Forest, 7.32N/36.31E, VI.1963, R. Linnavuori (MZHF); 1 ex., Shashamaanni, VI.1963, R. Linnavuori (MZHF); 4 ex., Addis Abeba, VII.1963, P. M. Schroeder (USNM); 1 ex., Shoa Prov., Wolisso, 8.32N/38.00E, VI.1971, R. O. S. Clarke (MRAC); 1 ex., Belleta Forest, 40 km SW Jimma, V.1971, R. O. S. Clarke (MRAC); 1 ex., Gibbie Riv., 175–185km SW Addis Abeba, V.1971, R.O.S. Clarke (MRAC); 1 ex., Gojeb river valley, 80 km SW Jimma, 7.20N/37.21E, 1650 m, VII.1971, R. O. S. Clarke (MRAC); 1 ex., Illubador Prov., 8 km N of Bedelle, 8.27N/36.20E, 1800 m, V.1972, R. O. S. Clarke (MRAC); 1 ex., Gemu Gofa Prov., Chencha, Gughé Mts., 6.12N/37.30E, 2800 m, IX.1972, R. O. S. Clarke (MRAC); 1 ex., Shoa, Awash Station, 6.58N/35.46E, IX.1973, G. de Rougemont (MRAC); 1 ex, Jimma, 7.40N/36.50E, II.1974, H. Silfverberg (MZHF); 6 ex., Addis Abeba, II.1974, H. Silfverberg (MZHF); 3 ex., Harage Alemaya, 9.23N/41.56E, II.1974, H. Silfverberg (MZHF); 2 ex., Kaffa Shebe, 7.40N/36.35E, II.1974, H. Silfverberg (MZHF); 4 ex., Arba Minch, 6.02N/37.33E, III.1974, H. Silfverberg (MZHF); 6 ex., Lake Langano, 7.38N/38.42E, sweep-netted, X.1980, A. Demeter (HNHM); 7 ex., Shafartak Bridge, Blue Nile, Abbai Gorge, 10.05N/38.18E, sweep-netted, X.1980, A. Demeter (HNHM); 4 ex., Koka, 8.20N/38.40E, sweep-netted, X.1980, A. Demeter (HNHM); 1 ex., Sodere, 8.24N/39.22E, sweep-netted, XI.1980, A. Demeter (HNHM); 8 ex., Akaki river, 8.50N/38.43E, sweep-netted, XI.1980, A. Demeter (HNHM); 1 ex., Awash NP, 11.30N/41.40E, sweep-netted, XI.1980, A. Demeter (HNHM); 1 ex., env. Pastoria, IX.1984, L. Medvedev (CMe); 2 ex., Gambella, 8.15N/34.35E, XI.1986, L. Medvedev (CMe); 1 ex., 30 km NW Gambella, XII.1986, L. Medvedev (CMe); 2 ex., pr. Illubabur, 20 km E Abobo, 7.51N/34.40E, XII.1986, L. Medvedev (CMe); 7 ex., Addis-Abeba, 2700, VIII.1988, X.–XI.1990, L. Medvedev (CMe); 1 ex., Sabata, 2000 m, XII.1988, L. Medvedev (CMe); 2 ex., Shoa, Debre Zeyt, 10.35N/35.48E, V.1989, Werner, coll. Döberl (CBe); 1 ex., Shewa, Rift Asella Valley, 7.57N/39.08E, III.–V.1989, Dèdoch (CBz); 17 ex., Ambo, 11.15N/39.34E, X.1990, *Acacia*, L. Medvedev (CMe); 2 ex., Arsi, reg. Mondo genet, 7.30N/39.30E, 1850 m, XIII.1990, Werner, coll. Döberl (CBe); 2 ex., Shoa, Lake Langano, 1600 m, VI.1990, Werner (MZUF); 8 ex., Shewa, Debre Lib., 9.04N/38.05E, 2500 m, III.1997, M. v. Tschirnhaus (ZFMK). – **Gabon:** 1 ex., Kankan, 0.02S/12.14E, VIII.1937, L. Berland (MNHN). – **Gambia:** 6 ex., Ht. Gambie, 13.15N/16.00W, II.–I II.1901, E. Laglaize (MNHN); 3 ex., Kouroussa, 10.40N/9.52W, XI.1995, Lange (CBe). – **Ghana:** 1 ex., Gold Coast (BMNH). – **Guinea:** 2 ex., Dalaba, 10.47N/12.12W, XII.1910, A. Chevalier (MNHN); 2 ex., Dalaba, 1200 m, VIII.1945, H. Durand (MNHN); 4 ex., Seredou, 8.23N/9.23W, IV.1975, A. Zott, lux (ZMHB); 8 ex., Tabuna, 9.31N/12.26W, IX.1983, III.1984, C. B. Myrzin (CMe); 4 ex., Telimela, II.1984, C. B. Myrzin (CMe); 1 ex., Kotento Yoko, III.1984, C. B. Myrzin (CMe). – **Guinea-Bissau:** 6 ex., Bolama, 11.33N/15.37W, VI.–XII.1899, L. Fea (MCSN); 1 ex., Contubo, 12.04N/15.23W, I.1938, coll. Laboissière (MRAC); 1 ex., Missão da Guiné, Aldeia de Cuor, II.1946, Dr. E. Frade (IICT). – **Ivory Coast:** 1 ex., Ashante, 7.10N/1.40W, Baly coll. (BMNH); 1 ex., Dimbroko (MHNH); 1 ex., G. Melou (MNHN); 2 ex., Haut Sassandra, pays Youra, 4.50N/6.00W, V.1910, F. Fleury, A. Chevalier (MNHN); 3 ex., Haut Sassandra, pays Dyola, 4.40N/6.20W, 1910, F. Fleury, A. Chevalier (MNHN); 2 ex., Danané, 7.19N/8.06W, I.1939, L. Chopard (MNHN); 4 ex., Adiopodoumé, II., X., XII.1947, Ch. Primot (MNHN); 1 ex., Adiopodoumé, IX.1952, coll. P. Cachan (MNHN); 1 ex., Akandjé, 5.24N/3.54W, I.1962, E. Lavabre (MNHN); 9 ex., Bingerville, 5.20N/3.52W, VI., IX–X.1962, III.1964, J. Decelle (MRAC); 1 ex., Zepreghé, Daloa, 6.56N/6.28W, IX.1962, J. Decelle (MRAC); 6 ex., Koun-Abronso, 7.31N/3.15W, XI.1961, I.1962, J. Decelle (MRAC); 2 ex., Nguessankro, Bougounanou, 7.57N/5.08W, X.1963, J. Decelle (MRAC); 1 ex., Ferkessédougou, 9.20N/5.00W, V.1964, J. Decelle (MRAC); 2 ex., Foro-Foro, 7.59N/5.03W, IX.1973, R. Linnavuori (MZHF); 2 ex., Man, X.1973, R. Linnavuori (MZHF); 16 ex., Comoe NP, 8.75N/3.80W, VI.–VII.1997, C. Mody (ZFMK). – **Kenya:** 2 ex., Kenia, Varendorff, coll. Kraatz (DEI, ZMUH); 1 ex., Nairobi, Ngong Forest, 1.22S/36.40E, 1900 m (IRSNB); 2 ex., Kibwezi, 2.25S/37.58E, XI.1887, G. Scheffler (ZMHB); 2 ex., Escarpment, 6500–9000 ft, IX.1900–IV.1901, W. Doherty (MNHN); 1 ex., Simba, 3350 ft, IV.1911, S. A. Neave (BMNH); 2 ex., Voi, 3.23S/38.35E, II.1912, S. A. Neave (BMNH); 1 ex., Ramissi, XI.1915, Methner (ZMHB); 1 ex., Tana River, VI.1915, G. Babault (MNHN); 1 ex., Fort Hall, 0.45S/37.00E, XII.1919, Patrizi (MCSN); 1 ex., Kisumu, 0.06S/34.45E, 3756 ft, XI.1920, A. F. J. Gedye (BMNH); 1 ex., Nairobi, 1.17S/36.50E, XI.1920, A. F. J. Gedye (NMK); 3 ex., Chania Falls, Thika, 1.03S/37.05E, 5050ft., I.1921, A. F. J. Gedye (NMK); 2 ex., Nairobi, 1.17S/36.50E, V.1921, VI.1937, A. F. J. Gedye (NMK); 1 ex., Kabete, 1.16S/36.43E, VIII.1921, H. E. Box (BMNH); 1 ex., Machakos, 2.00S/37.40E, XII.1923, J. W. Hunt (NMK); 1 ex., Ngong KC, 1.22S/36.40E, VIII.1925, A. F. J. Gedye (NMK); 1 ex., Gasi, 4.25S/39.30E, XI.1927, Dr. van Someren (NMK); 1 ex., Thika, 1.03S/37.05E, IV.1930, coffee (BMNH); 1 ex., Yala River près Kisumu, 0.04S/34.05E, X.1930, coll. G. Babault (MNHN); 2 ex., Kaimosi, 0.12N/34.57E, III.-IV.1932, A. Turner (NMK); 2 ex., Marakwet, Kigeyo Escarpment, 1.05N/35.37E, 1932–1933, Miss. de l'Omo, C. Arambourg et al. (MNHN); 3 ex., Elgon Saw mill, Mt. Elgon, ver est, 1.05N/34.40E, 2470 m, 1932–1933, Miss. de l'Omo, C. Arambourg et al. (MNHN); 1 ex., Thika Falls, Kukiyu, 1700 m, 1932–1933, Miss. de l'Omo, C. Arambourg et al. (MNHN); 1 ex., Suam fishing hut, Mt. Elgon vers est, 1.06N/34.33E, 2400 m, 1932–133, Miss. de l'Omo, C. Arambourg et al. (MNHN); 1 ex., Nairobi, 1660 m, 1932–1933, Miss. de l'Omo, C. Arambourg et al. (MNHN); 1 ex., Lower Tana, Sabaki, 3.09S/40.07E, IV.–V.1932, Turner-Mac Arthur (NMK); 2 ex., Kisumu, IV.1936, H. J. A. Turner (NMK); 2 ex., Kanziko, 1.49S/38.15E, IX.1936, V.1937, Mac Arthur (NMK); 1 ex., Athi Falls, VII.1937, A. F. J. Gedye (NMK); 1 ex., Karakuta, 1.03S/36.57E, VIII.1937, R. E. Toker (NMK); 6 ex., Kitui, 1.22S/38.01E, X.1937, R. Toker (NMK); 2 ex., Lake Baringo, 0.38N/36.05E, 3400 ft, I.1938, D. G. MacInnes (NMK); 1 ex., Stoneham, E. Surr. Estate, II.1938 (NMK); 1 ex., Malakisi, 0.41N/34.25E, 1600 m, II.1938, Å. Holm (NHRS); 1 ex., Mt. Elgon, River Swam, 1.48N/35.09E, 2000 m, II.1938, Å. Holm (NHRS); 2 ex., Kaptega Estate, 1.11N/34.46E, 2050 m, IV.1938, Å. Holm (NHRS); 1 ex., Thika Dist., 1.00S/37.20E, IV.1938, S. Blom Bjorner (NMK); 63 ex., Chyulu Hills, 2.35S/37.50E, 5600 ft, IV.–VII.1938, Coryndon Museum (62 ex. NMK, 1 ex. USNM); 3 ex., Thika, 1.04S/37.02E, X.1937, X.1938, S. Blom Bjorner (1 ex. BMNH, 2 ex. NMK); 2 ex., Kabete, 1.16S/36.43E, 5800 ft, XII.1938, I.1939, Mac Innes (BMNH, NMK); 2 ex., Malindi, 3.13S/40.07E, V.1940, G. W. Jeffery (BMNH, NMK); 1 ex., Karura Forest, 1.30S/36.46E, II.1941 (NMK); 2 ex., Nairobi, IV.1943, Meneghetti (NMK); 1 ex., Kaiti River, 1.45S/37.42E, II.1947, v. Someren (BMNH); 1 ex., Taita Hills, 3.25S/38.20E, VIII.1947, van Someren (NMK); 1 ex., Mombasa, 4.04S/39.40E, IX.1947, T. H. E. Jackson (NMK); 1 ex., Mombasa, VIII.1948, A. F. J. Gedye (NMK); 1 ex., Kange-Ngomeni Road, 0.50S/38.25E, V.1951, sweep net attached to car 6 ft above ground (BMNH); 2 ex., Diani Beach, 4.18S/39.35E, VII.–VIII.1951, N. L. H. Krauss (BMNH); 1 ex., Nairobi, I.1953, E. Pinhey (NMK); 1 ex., Taveta, 15 km E, 3.23S/37.42E, VII.1968, N. Sanfilippo (MCSN); 8 ex., Nairobi, VIII.–X.1969, M. P. Cliften (NMK); 1 ex., Kisumu, XII.1970, A. E. Stubbs (BMNH); 1 ex., Tiwi Beach, 4.14S/39.35E, V.1971, B. D. Valentine coll. (BPBM); 1 ex., L. Naivasha, Crescent Island, 0.54S/36.37E, 6200 ft, I.1972, C. F. Huggins (BMNH); 3 ex., Kora Rock, Tana River Exp., VII.1976, tilley lamp (NMK); 10 ex., Kaptega, 1980 m, I.–II.1979, T. E. Leiler (NHRS); 1 ex., Naro Moru, 0.10S/37.01E, VIII.1979 (NNML); 4 ex., Stony Athi, 1.35S/37.00E, VI.1980, D. G. Furth (USNM); 5 ex., Langata Forest, 1.20S/36.47E, VI.1980, D. G. Furth (USNM); 2 ex., Nairobi, 1850 m, III.1981, E. Räsänen, at light (MZHF); 3 ex., Kora NR, 0.38S/37.00E, Base Camp, VIII.1983, M. Clifton (NMK); 2 ex., Nairobi, IX.1987, B. L. Parker (NMK); 1 ex., Kakamega Forest, 0.18N/34.53E, IV.1991, R. Copeland (NMK); 5 ex., Mt. Elgon NP, nr. Chepanyalli Cave, dry evergreen montane forest, 2500 m, I.1992, O. Merkl & G. Várkonyi (HNHM); 2 ex., Arabuko Sokoke FR, 3.20S/39.52E, IX.-X.1992, L. Bartolozzi (MZUF); 1 ex., Taita Distr., Bura, 3.30S/38.18E, VI.1994, L. Bartolozzi, B. Cecchi, A. Sforzi (MZUF); 2 ex., Masai Mara, 1.25S/34.55E, 1600 m, VI.1994, L. Bartolozzi (MZUF); 1 ex., Ngong Hills, Nairobi Res. Stat., XI.1995, R. Copeland (NMK); 1 ex., Kitale, Kapenguria, 2300 m, XII.1995, M. Snizek (MIZT); 1 ex., Taita Hills, Rongo Forest, 3.21S/38.26E, X.–XI.1996, Malaise trap, ICIPE (NMK); 1 ex., Taita Hills, Wundanyi, XI.1997, M. Snizek (MIZT); 1 ex., Nairobi, Langata, 1.20S/36.46E, 1650 m, I.1999, Th. Wagner, insecticidal fogging of *Teclea simplicifolia* (ZFMK); 1 ex., Taita Hills, n. Wundanyi, 3.24S/38.22E, 1660 m, III.1999, Th. Wagner (ZFMK); 1 ex., Mwingi, Ngumi, 0.56S/38.04E, XI.1999, M. Snizek (MIZT); 21 ex., Kakamega Forest, Kaimosi, 0.12N/34.57E, IX.2001, Th. Wagner et al. (ZFMK); 106 ex., Kakamega Forest, nr. Buyangu, 0.13N/34.44E, II., IV.2002, light trap (ZFMK); 5 ex., Chogoria, 0.14S/37.37E, 1800 m, X.2002, Co. & Th. Wagner (ZFMK). – **Malawi:** 1 ex., SW shore L Nyasa, between Ft. Johnson & Monkey Bay, 1650 ft, II.–II.1910, S. A. Neave (BMNH); 1 ex., W shore L Nyasa, between Domira Bay & Kotakota, 13.35S/34.27E, XI.1910, S. A. Neave (BMNH); 9 ex., Mlanje, 16.05S/36.29E, IV.–VII.1913, S. A. Neave (BMNH); 1 ex., Side of Mt. Mlanje, 16.00S/36.30E, 3000–4000 ft, XII.1913, S. A. Neave (BMNH); 3 ex., Zomdu Plateau, N. L. H. Krauss, B.M. 1957–3458 (BMNH); 1 ex., Mt. Mulanje, 15.58S/35.38E, 900 m, XII.1983, Bellamy (TMSA); 1 ex., Nyiaka Plateau, Chilinda, 10.19S/33.48E, 2250 m, IV.1991, D. Lachaise (MNHN). **Mali:** 1 ex., cercle Kandia, 14.46N/11.30W, 1935, P. Malzy (MNHN); 14 ex., IRCT, M'Pesoba, 12.40N/5.43W, IX.–X.1969, VIII.–IX.1970, G. Pierrard (MRAC); 9 ex., Fana, 12.47N/6.57W, VIII.–IX.1969, VIII.1970, G. Pierrard (MRAC); 1 ex., Kassorola, 14.08N/7.25W, X.1969, G. Pierrard (MRAC); 5 ex., Lutana, IX.1969, VIII.1970, G. Pierrard (MRAC). – **Moçambique:** 1 ex., Mozamb. Nyassa, Thelwall (BMNH); 1 ex., Zambese, 1882, Durand (MNHN); 1 ex., Beira, 19.49S/34.52E, III.1903, P. A. Sheppard (BMNH); 1 ex., Vallée du Revoué, env. d'Andrada, 18.52S/32.53E, XI.1905, G. Vasse (MNHN); 2 ex., Chibababa, Lower Buzi R., XII.1906, C. F. M. Swynnerton (BMNH); 2 ex., Vallée du Pongoué, Guengére, 18.45S/33.40E, VI.1906, G. Vasse (MNHN); 2 ex., Prov. du Gorongoza, Tendo du Sungoue, 18.32S/34.15E, 40 m, X.1907, G. Vasse (MNHN); 1 ex., Prov. du Gorongoza, Forêt Dinhanoonde, 360 m, X.1907, G. Vasse (MNHN); 2 ex., Zambèze, Nova Choupanga pr. Chemba, 17.10S/35.00E, IV.1929, P. Lesne (MNHN); 1 ex., env. de Beira, Manga, 19.45S/34.50E, VII.1929, P. Lesne (MNHN); 1 ex., Ugano, Matengo-Hochland, wsw. V. Songen, 12.51S/35.48E, XII.1935, Zerny (HNHM); 1 ex., Missão Zoológica, Mufo, 10.37S/34.08E, VII.1948 (IICT); 1 ex., Missão Zoológica, Tica, 19.00S/33.07E, VII.1948 (IICT); 3 ex., Missão Zoológica, Gondola, 19.05S/33.39E, VIII.1948 (IICT); 7 ex., Missão Zoológica, Bengo, 19.04S/33.37E, VIII.1948 (IICT); 1 ex., Missão Zoológica, Zinai, VIII.1948 (IICT); 1 ex., Missão Zoológica, Cosme, Vila Coutinho, 18.40S/34.24E, IX.1948 (IICT); 2 ex., Missão Zoológica, Tambara, 16.44S/34.15E, IX.1948 (IICT); 1 ex., Missão Zoológica, Lifidzi, 14.33E/34.14E, IX.1948 (IICT). – **Nigeria:** 1 ex., Gomba, 12.55N/8.38E, Mataoro lakes, I.1929, Dr. Ll. Lloyd (BMNH); 1 ex., NW state, Kontagora River, 10.24N/5.29E, 3 mls. from Niger, VIII.1970, P. H. Ward, on semicultivated land (BMNH); 4 ex., SE State, Obudu Cattle Ranch, 6.38N/9.55E, VIII.1974, R. Linnavuori (MZHF). – **Rwanda:** 1 ex., Bugarama, 2.27S/29.29E, I.1926, H. Schouteden (MRAC); 1 ex., Gabiro, 1.53S/30.23E, X.1932, L. Burgeon (MRAC); 1 ex., Bugarama, V.1951 (IRSNB); 2 ex., Kisenyi, 1.41S/29.15E, VIII.1952, A. E. Bertrand (MRAC); 1 ex., Shangugu, 2.29S/28.54E, 1500 m, IV.1953, P. Basilewsky (MRAC); 1 ex., Kayove, terr. Kisenyi, 1.53S/29.21E, 2000 m, II.1953, P. Basilewsky (MRAC); 1 ex., terr. Ruhengeri, Kagogo, 1.22S/29.46E, 1900 m, I.1958, P. Basilewsky (MRAC); 3 ex., est Muhavura, 1.23S/29.40E, 2100 m, I.1958, P. Basilewsky (MRAC); 2 ex., env. Astrida, 2.36S/29.44E, 1954/1955, G. Foucart (MRAC); 1 ex., Nyarubuye, 1.58S/29.59E, III.1972, F. Cuypers (MRAC); 1 ex., Cyangugu, Nyakabuye, 2.10S/29.31E, X.–XI.1983, H. Mühle (CKi); 2 ex., Gako, Kibungo, 2.12S/30.27E, 1400 m, IX.1984, H. Mühle (CKi); 4 ex., Kigali, 2.00S/29.40E, X.1970, coll. Roggeman (CBe); 1 ex., Gifurwe, 1.33S/29.48E, IV.1972, coll. Roggeman (CBe); 2 ex., Mt. Kigali, V.1972, coll. Roggeman (CBe); 2 ex., Icyanya, X.1973, coll. Roggeman (CBe); 2 ex., Gisenyi, 1.41S/29.15E, IV.1973, coll. Roggeman (CBe); 1 ex., Tumba, 1.41S/29.57E, V.1973, coll. Roggeman (CBe); 3 ex., Nasho I, 2.02S/30.43E, VIII.1988, E. Fischer (ZFMK); 41 ex., Rusumo, Ibanda Makera, 2.13S/30.42E, X.1993 / IX.2002, Th. Wagner, partim insecticidal tree fogging of *Lannea fulva, Teclea nobilis* (ZFMK). – **Senegal:** 1 ex., Kati, 13.54N/14.57W, VII.1913, coll. Clavareau (MRAC); 1 ex., Sinthiou-Maleme, 13.03N/15.18W, VIII.1939, J. Risbec (BMNH); 2 ex., Guede, 14.53N/15.52W, II.1946 (BMNH); 7 ex., Sébikotane, 14.45N/17.05W, XI.–XII.1945, III.1946, VII.1947, H. Durand (MNHN); 1 ex., Diakéne, 12.27N/16.37W, X.1960, Sala (MCTB); 1 ex., Sangalkam, 14.47N/17.13W, VIII.1967, A. Descarpentries et al. (MNHN); 1 ex., Sebikotane, VIII.1971, A. Villiers (MNHN). – **Sierra Leone**: 1 ex. (BMNH); 1 ex., *M. pulchella* Klug, Jac. coll. (BMNH); 1 ex., Baly coll. (BMNH); 1 ex., ex coll. J. Weise (ZMHB); 2 ex., Rhobomp, coll. Kraatz / coll. Jacoby (BMNH, DEI); 1 ex., ex coll. J. Weise (ZMHB); 1 ex., VIII.1892, Rev. D. Z. Morgan, *duplicata* Sahlberg (BMNH); 1 ex., Kaballa, 9.35N/11.33W, V.1912, J. J. Simpson (BMNH). – **Somalia:** 2 ex., Mogadiscio, 2.04N/45.22E, ex. coll. Breuning (MRAC); 1 ex., nr. Hargeissa, VI.1963, Linnavuori (MZHF); 1 ex., Mogadiscio, III.1974 (CMa). – **Sudan:** 1 ex., Latuka, 4.39N/32.33E, 1918, J. R. Yardley (IRSNB); 1 ex., W. Darfur, N. Jebel Murra, 10.21N/23.24E, 5600 ft., VII.1932, M. Steele (BMNH); 1 ex., Upper Nile, Malakal, 9.32N/31.39E, I.1963, Linnavuori (MZHF); 1 ex., Equatoria, Lotti Forest, 4.00N/32.32E, III.1963, R. Linnavuori (MZHF); 3 ex., Equatoria, Imatong Mts. nr. Gilo, 4.03N/32.51E, III.1963, Linnavuori (MZHF); 1 ex., Equatoria, Kapoeta-Boma, 4.46N/33.35E, II.1963, Linnavuori (MZHF); 1 ex., Jebel Marra, 12.55N/24.12E, Gallery forest, on dry rock in stream, IX.1983, R. Moore (BMNH). – **Tanzania:** 1 ex., Usambara, Nguela, 4.45S/38.30E (IRSNB); 1 ex., Moshi, 3.20S/37.21E, coll. Hauser (IRSNB); 1 ex., Zanzibar, 6.10S/39.12E, Raffray (MNHN); 12 ex., Ukerewe Island, 2.09S/32.52E, Conrads (4 ex. IRSNB, 8 ex. NMK); 1 ex., Arusha-Chini, Katona, 3.09S/38.26E (NMK); 1 ex., inter Marti et Arusha, Katona (NMK); 1 ex., Kibosho, Katona (NMK); 2 ex., Montes Lettema, Katona (NMK); 1 ex. Kilimandjaro, 3.04S/37.22E, Katona (NMK); 1 ex., Kilimandjaro, Bornemissza (NMK); 1 ex., Kilimandscharo, Dschagga-Land, Madchame, T. Paesler (ZMHB); 1 ex., "Kilimandjaro / ex. coll. Weise / Type / *Monolepta sjöstedti* m [invalid type] (ZMHB); 1 ex., "Kilimandjaro, Sjöstedt. 1905-6 / Kibonoto 00-1900 / ex. coll. Weise / Type [invalid type] (ZMHB); 1 ex., Kirumba b. Muansa, 2.31S/32.54E, Holtz (ZMHB); 4 ex., Parek, 2000 m, Ch. Schröder (ZMHB); 4 ex., Kikuiru, Massaisteppe, Ch. Schröders (ZMHB); 4 ex., Kilimandjaro, Sjöstedt (ZMHB); 1 ex., Kilimandjaro, Sjöstedt, Kibonoto, 1'–1200 m, IV. (NHRS); 1 ex., Kwai, 4.44S/38.21E, Paul W. (NHRS); 2 ex., Usambara, Derema, 4.45S/38.30E, 850 m, IX.-X.1891, Conradt (ZMHB); 2 ex., Langenburg, Ineteyanur nya a. Nyassa, 9.01S/33.39E, VI,1898, Fülleborn (ZMHB); 1 ex., Rungwe, 9.15S/33.40E, II.1899, Stolz (ZMHB); 1 ex., W.-Pemba, III.1903, Voeltzkow (ZMHB); 1 ex., Pemba, Chake-Chake, 5.15S/39.45E, IV.1903, Voeltzkow (ZMHB); 1 ex., Pemba, Fundu, 5.03S/39.39E, IV.1903, Voeltzkow (ZMHB); 2 ex., Moshi, 3.20S/37.21E, 1905, Fl. Rau, Katona (NMK); 1 ex., Amani, 5.09S/38.36E, X.-XII.1905, 900 m, Ch. Schröder (ZMHB); 7 ex., Arusha-Ju, 3.22S/36.38E, XI.1905, Katona (NMK); 2 ex., Papyrus-Sumpf, süd ö. Kilimandjaro, I.1906, Ch. Schröder (ZMHB); 2 ex., Panganisteppe, Mombo-Masinde, I.1906, Ch. Schröder (ZMHB); 1 ex., Amani, II.1906, Vosseler (ZMHB); 1 ex., D. Sambesi Geb., X.1906, F. Seiner (ZMHB); 1 ex., Shirati, 1.08S/33.59E, II.1909, Katona (NMK); 6 ex., Lake Ippe, 3.35S/37.45E, 1910, Gotsch (NHMW); 1 ex., Meru, Ngare na Nyuki, 3.09S/36.51E, Sjöstedt (NHRS); 3 ex., Usangu Distr., 8.30S/34.15E, XI.–XII.1910, S. A. Neave (BMNH); 1 ex., Kilimandscharo, 2500–3000 m, am Bismarckhügel oberh. Marangu, südl. Mawenzi am Fuße der Hochweiden, II.1912, Ch. Schröder (ZMHB); 1 ex., Nord-Uluguru, 7.05S/37.35E, 1400-1900 m, II.1914, Methner (ZMHB); 4 ex., Kirumba, XI.1914, II.1915, Holtz (3 ex. ZMHB, 1 ex. ZMUH); 2 ex., Narobi bei Tanga, 5.05S/39.02E, IV.1915, Methner (ZMHB); 2 ex., Muansa, VIII.1915, Holtz (ZMHB); 1 ex., K-D River Camp, Noisinak Bridge, 3500 ft, V.1916, W. A. Lamborn (BMNH); 5 ex., E. Tanganyika, Kigoma, 4.52S/29.36E, IX.1918. R. Mayné (MRAC); 1 ex., Nata, 2.00S/34.24E, II.1960, Dr. Szunyoghy (NMK); 1 ex., Bunduki, Uluguru Mts., 7.05S/37.35E, 6000 ft, XI.1948, J. G. Williams (NMK); 5 ex., Bunduki, Uluguru Mts., Moy. Mgeta, 7.02S/37.34E, 1300 m, IV.-V.1957, P. Basilewsky & N. Leleup (MRAC); 4 ex., Mt. Hanang, 2200–2500 m, 4.26S/35.24E, V.1957, P. Basilewsky & N. Leleup (MRAC); 1 ex., Ngorongoro Rest Camp, 3.11S/35.23E, 2400–2500 m, VI.1957, P. Basilewsky & N. Leleup (MRAC); 4 ex., Mt. Kilimandjaro, Marangu, 3.17S/37.31E, 1600–1700m, VII.1971, P. Basilewsky & N. Leleup (MRAC); 2 ex., Mulukulazo, III.1969, I. A. D. Robertson, sweep net (BMNH); 1 ex., Ngorongoro Crater, 1500 m, Berger et al. (MRAC); 1 ex., Morogoro, 6.49S/37.40E, 600 m, V.–VI.1971, L. Berger et al. (MRAC); 1 ex., Uluguru Mts., Kiroka, 6.50S/37.49E, 725 m, V.1971, L. Berger et al.(MRAC); 1 ex., Uluguru Mts., Kinola, 1500–1750 m, VI.1971, L. Berger et al.(MRAC); 1 ex., Uluguru Mts., Lukwangule Plateau, 2400–2600 m, VII.1971, L. Berger et al. (MRAC); 5 ex., Uluguru Mts., Chenzema, 7.06S/37.35E, 1700 m, VII.1971, L. Berger et al.(MRAC); 2 ex., Morogoro, I.1974, H. Silfverberg (MZHF); 1 ex., Uzungwa Mts., Mwanihana F. above Sanje, 8.20S/35.58E, 1000 m, VIII.1982, M. Scholtze & N. Scharff, pitfall trap (ZMUC); 1 ex., Uzungwa Mts., Chita FR, 8.31S/35.56E, 750 m, X.1984, M. Scholtze & G. Petersen (ZMUC); 1 ex., Morogoro, 6.49S/37.40E, University Campus, I.1988, T. Pócs, at light (NMK); 1 ex., Uluguru Mts., IV.1991, Werner (CDö); 2 ex., Pangani Falls Forest, 5.20S/38.40E, I.-III.1993 (ZMUC); 11 ex., Mkomazi G. R., 4.10S/38.10E, *Acacia tortilis, Acacia mellifera, Acacia recifiens, Acacia senegal, Lannea stuhlmanni, Melia volkensii, Terminalia sp.A* canopy sampling, VII.–VIII.1994, G. McGavin (BMNH); 150 ex., Mufindi Distr., Iringa, Ut´zungwa Scarp FR, 8.31S/35.54E, 750 m, III.1996, McKamey et al., canopy UV and fog (ZMUC); 2 ex., 12 km O Iringa, Little Ruawa Riverside Camp, 7.48S/35.48O, IX.2002, U. Heinig (CHe). – **Togo:** 8 ex., Bismarckburg, 8.15N/0.55E, XII.1892, V.–VI.1893, L. Conradt (ZMHB); 1 ex., Misahöhe, 6.59N/0.40E, VI.1894, F. Baumann (ZMHB). – **Uganda:** 1 ex., Mulangu, 0.30N/32.02E, ex. Staudinger (MRAC); 2 ex., Bussu, Busoga, 0.45N/33.30E, II.1909, 1910, E. Bayon (MCSN); 1 ex., Mt. Kokanjero, SW of Elgon, 6400 ft, VIII.1911, S. A. Neave (BMNH); 1 ex., Siroko R. nr W foot of Mt. Elgon, 1.29N/34.14E, 3600 ft, VIII.1911, S. A. Neave (BMNH); 2 ex., between Seziwa R. & Kampala, VIII.1911, S. A. Neave (BMNH); 1 ex., Daro/Durro Forest, Toro, 4000–4500 ft., X.1911, S. A. Neave (BMNH); 1 ex., Mpanga Forest, Toro, 0.15N/32.05E, 4800 ft, XI.1911, S.A. Neave (BMNH); 1 ex., Tero Forest, SE Buddu, 0.50S/31.40E, 3800 ft, IX.1911, S. A. Neave (BMNH); 1 ex., Bugoma, Forest, Unyoro, 1.15N/30.53E, 3700 ft, XII.1911, S. A. Neave (BMNH); 2 ex., Kafu R. near Hoima, Kampala Rd., 1.25N/31.22E, 3500 ft, XII.1911, S. A. Neave (BMNH); 1 ex., Between Mitiana & Entebbe, 0.24N/32.03E, 3800 ft., I.1912, S. A. Neave (BMNH); 2 ex., N of L. Isolt, 3700 ft., I.1912, S. A. Neave (BMNH); 1 ex., Shores of L. Isolt, Wamala, 0.04N/31.54E, 3800 ft, I.1912, S. A. Neave (BMNH); 1 ex., S foot & slopes of Mt. Elgon, 5100–5800 ft, 1912 (BMNH); 1 ex., Hima Riv., 0.18N/30.10E, IV.1912, Dr. Bayer (MRAC); 1 ex., Tero, 0.50S/31.40E, VII.1912, C. C. Gowdey (ZMUH); 3 ex., Mujenje, VIII.1913, Katona (NMK); 9 ex., Kampala, 0.19N/32.35E, X.1920, IX.1947, IV.-VI.1948, XII.1925, A. F. J. Gedye (NMK); 2 ex., Jinja, 0.19N/33.59E, VIII.1924, VIII.1926, A. F. J. Gedye (NMK); 1 ex., Buamba, 7000 ft, X.1926 (ZMUH); 9 ex., Kiryanga, 1.06N/31.04E, IV.1927, H. Hargeraves (5 ex. BMNH, 4 ex. ZMUH); 1 ex., Busongoro, 0.05N/30.00E, XII.1927, G. D. H. Carpenter (BMNH); 1 ex., Budongo, 1.45N/31.35E, IX.1932, T. Jackson (BMNH); 1 ex., Ruwenzori Range, Kilembe, 0.12N/30.00E, 4500 ft., XII.1934-I.1935, F. W. Edwards (BMNH); 1 ex., Budongo F., 1.45N/31.35E, X.1936, A. F. J. Gedye (NMK); 1 ex., Bubulu, 0.56N/34.16E, X.1938, T. H. C. Taylor (BMNH); 1 ex., Kyagwe, 0.25N/32.50E, VI.1938, T. H. C. Taylor (BMNH); 1 ex., Kampala, 0.19N/32.35E, VI.1940, A. F. J. Gedye (NMK); 3 ex., W of Ruwenzori, 6000 ft, VII.1945, van Someren (1 ex. BMNH, 2 ex. NMK); 2 ex., Bwamba, 0.43N/30.04E, VII.–VIII.1946, VI.1948, v. Someren (NMK); 1 ex., Kampala, 3200 ft, XII.1946, A. F. J. Gedye (USNM); 2 ex., Bwamba Forest, 2500 ft., III.1948, J. G. Williams (NMK); 5 ex., Bwamba, Hakitengya, XI.1948, W. H. R. Lumsden, from fan trap (BMNH); 1 ex., Mafuga Forest, 1.03S/29.52E, III.–VI.1951, T. H. E. Jackson (NMK); 1 ex., Ruwenzori Range, Bugoye, 4500 ft, IX.1952, D. S. Fletcher (BMNH); 1 ex., Ruwenzori Range, Semliki F., 2850 ft, VIII.–IX.1952, D. S. Fletcher (BMNH); 1 ex., Kampala, XII.1952, A. F. Gedye (NMK); 1 ex., Katera, 0.42S/32.00E, XI.1953, T. H. E. Jackson (NMK); 1 ex., Jinja, 0.19N/33.59E, XII.1954-II.1955, P S. Corbet, M.V. light trap (BMNH); 2 ex., Bugiri, 0.34N/33.45E, 1400 m, P. VIII.1957, Basilewsky & N. Leleup (MRAC); 1 ex., Kawanda, 0.01S/31.29E, II.–III.1958, P. Whalley, M. V. light trap (BMNH); 2 ex., Entebbe, 0.05N/32.29E, III.1972, Falk (MRAC) 315 ex., Kibale Forest, 0.50N/31.06E, VII. VIII., X.1983, IV. V., VII., IX.–XII.1984, I., III.–IV. XII.1985, 1991, IX.1991, M Nummelin, sweep (MZHF); 265 ex., Budongo Forest nr. Sonso, 1.45N/31.35E, VI.1995, insecticidal canopy fogging of *Cynometra alexandri, Rinorea beniensis, Teclea nobilis, Trichilia rubescens*, Th. Wagner (ZFMK); 3 ex., Semliki Forest, 0.48N/30.09E, II.1997, U. Göllner (ZMHB); 15 ex., Semliki Forest, II.1997, Th. Wagner, insecticidal fogging of *Cynometra alexandri, Elais guinensis*, U. Göllner (1 ex. ZMHB, 14 ex. ZFMK); 5 ex., Nyabyeya, 1160 m, 1.40N/31.32E, IX.1997, Th. Wagner (ZFMK); 1 ex., Kibale Forest, nr. MUBS, VIII.1997, M. Boppré (ZFMK); 15 ex., Kibale NP, U. Kanyawara, 0.50N/31.06E, 1600 m, VIII.1998, L. Schmidt (ZFMK); 1 ex., Kasese, Queen Elisabeth NP, Mweya, 0.10N/30.05E, VIII.1998, I. Schmidt (ZFMK). **Zambia:** 3 ex., Niamadzi R., nr. Nawalia, VIII.1910, S. A. Neave (BMNH); 1 ex., Upper Luangwa R., 14.49S/19.06E, VII.–VIII.1910, S. A. Neave (BMNH); 3 ex., Caia, Zambesi, 17.49S/35.23E, X.1911, H. Swale (BMNH); 1 ex., Namwala, III.1913, H. C. Dolman (BMNH); 1 ex., Chilonga, 12.02S/31.21E, VII.1913, on *Citrus* trees infested with black aphids (BMNH); 10 ex., Mwengwa, 13.00S/27.66E, VII.–VIII.1914, H. C. Dollman (BMNH); 14 ex., Lukanga, 14,33S/27,48E, VII.1915, H. C. Dolman (BMNH); 1 ex., Kashitu, 13.45S/28.40E, N. of Broken Hills, VII.1915, H. C. Dolman (BMNH); 1 ex., N'Changa, 13.29S 30.27E, 1931, C. T. MacNamara (BMNH); 1 ex., Sesheke, 16.45S/24.20E, 950 m, III.–VI.1991, W. Slobbe (NNML); 3 ex., Kafue River, Rimo Marine Motel, 15.49S/28.12E, III.1993, U. Göllner (ZMHB). – **Zimbabwe:** 1 ex., Vumba Mts., Nebelwald, ca.1500 m, 19.06S/32.47E, III.2000, U. Heinig (CHe); 1 ex., Kariba, Mopani Bay Camp, 16.31S/28.49E, III.2000, R. Beenen (CBe); 1 ex., Chimanimani NP, 19.48S/32.52E, XII.1998, S. Bečvář (CBz); 1 ex. dto., A. Kudrna (CBe).

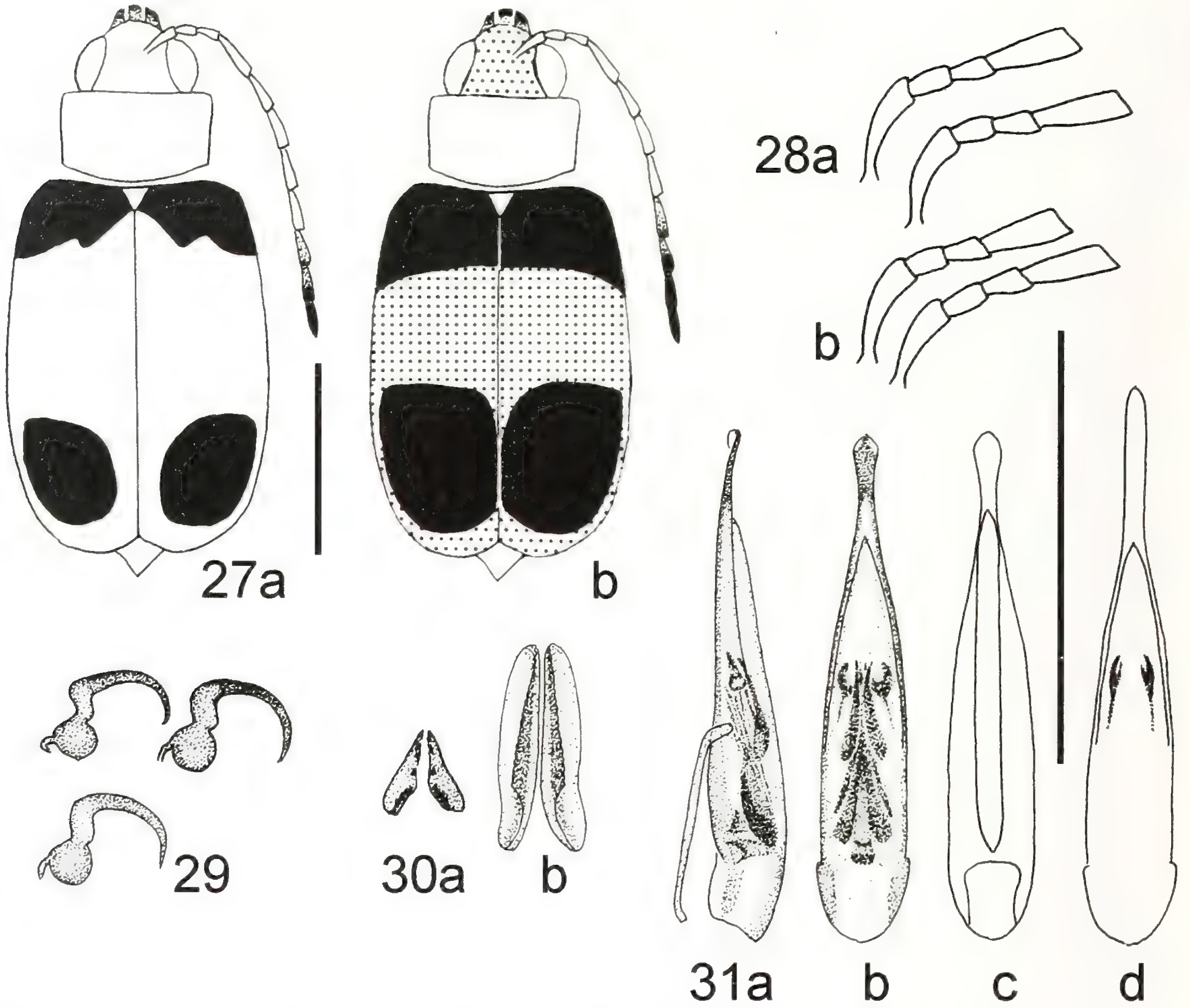
Monolepta ronbeeneni sp. n.

Description.

Total length. 3.10–3.60 mm (mean: 3.25 mm; n = 10).

Head. Yellow to yellowish-red, mouth-parts including palpi brownish (Fig. 27). Antennae pale yellow, last two to four antennomere brownish or black, all antennomeres very elongated (Figs 27, 28), length of antennomeres two to three 1.00–1.10 (mean: 1.04), length of antennomeres three to four 0.41–0.62 (mean: 0.46).

Thorax. Prothorax pale yellow to yellowish (Fig. 27). Pronotal width 0.85–1.05 mm (mean: 0.96 mm), pronotum broad, pronotal length to width 0.59–0.64 (mean: 0.61), very finely punctured. Elytra yellow to reddish-yellow, base with transverse black band, often undulate posteriorly (Fig. 27a), subapical usually with large ovate spot, which is often more brownish and not sharply delimited. Elytral length 2.30–2.80 mm (mean: 2.42 mm), maximal width of both elytra 1.45–1.75 mm (mean: 1.65 mm), maximal width of both elytra to length of elytron 0.66–0.71 (mean: 0.69). Scutellum yellow. Meso- and metathorax yellow to yellowish-red, rarely brownish, legs yellow.



Figs 27–31: *Monolepta ronbeeneni* sp. n. 27: colour pattern; 28: basal antennal articles (a: ♂, b: ♀); 29: three different spermathecae; 30: bursa-sclerites (a: dorsal, b: ventral); 31: median lobe (a: lateral, b: dorsal from Albertine Rift, c: dorsal from western Central Africa, d: ventral, without endophallic structures).

Abdomen. Yellow to yellowish-red.

Female genitalia. Spermatheca with small spherical nodulus, comparatively broad middle part and long, strongly curved cornu (Fig. 29). Dorsal part of bursa sclerites small, elongated triangular (Fig. 30a), ventral part very broad (Fig. 30b).

Male genitalia. Median lobe straight, very slender at apex, in specimens along the Albertine Rift apex slightly enlarged (Fig. 31b), specimens from western Central Africa apex parallel-sided (Fig. 31c). Tectum comparatively broad, ventral groove parallel-sided (Fig. 31d). Dorsal pair of median endophallic spiculae very strong, other median spiculae slender, ventral spiculae absent, lateral spiculae with large U-shaped apex (Fig. 31b), which is slenderer in most specimens from western Central Africa (Fig. 31c).

Distribution. Forests and savannas of northern Central Africa from northern and the Central African Republic to Uganda and Rwanda (Fig. 32).

Diagnosis. *Monolepta ronbeeneni* sp. n. is one of the smallest afrotropical *Monolepta* species. It is equal in size and antennal characters to *M. wittei* Laboissière, 1940, a species which differs in having throughout yellowish-red elytra, a black apical abdominal segment, very different male genital characters, and is restricted to Lake Kivu region at the Albertine Rift (WAGNER 2002). *Monolepta buquetii* can be easily distinguished by the short basal antennomeres, the short antennae, broader pronotum, it has no reddish-yellow elytral coloration and does not occur along the Albertine Rift. Only a very few specimens of *M. vincta* and *M. sharonae* sp. n. are as small as *M. ronbeeneni* sp. n., which

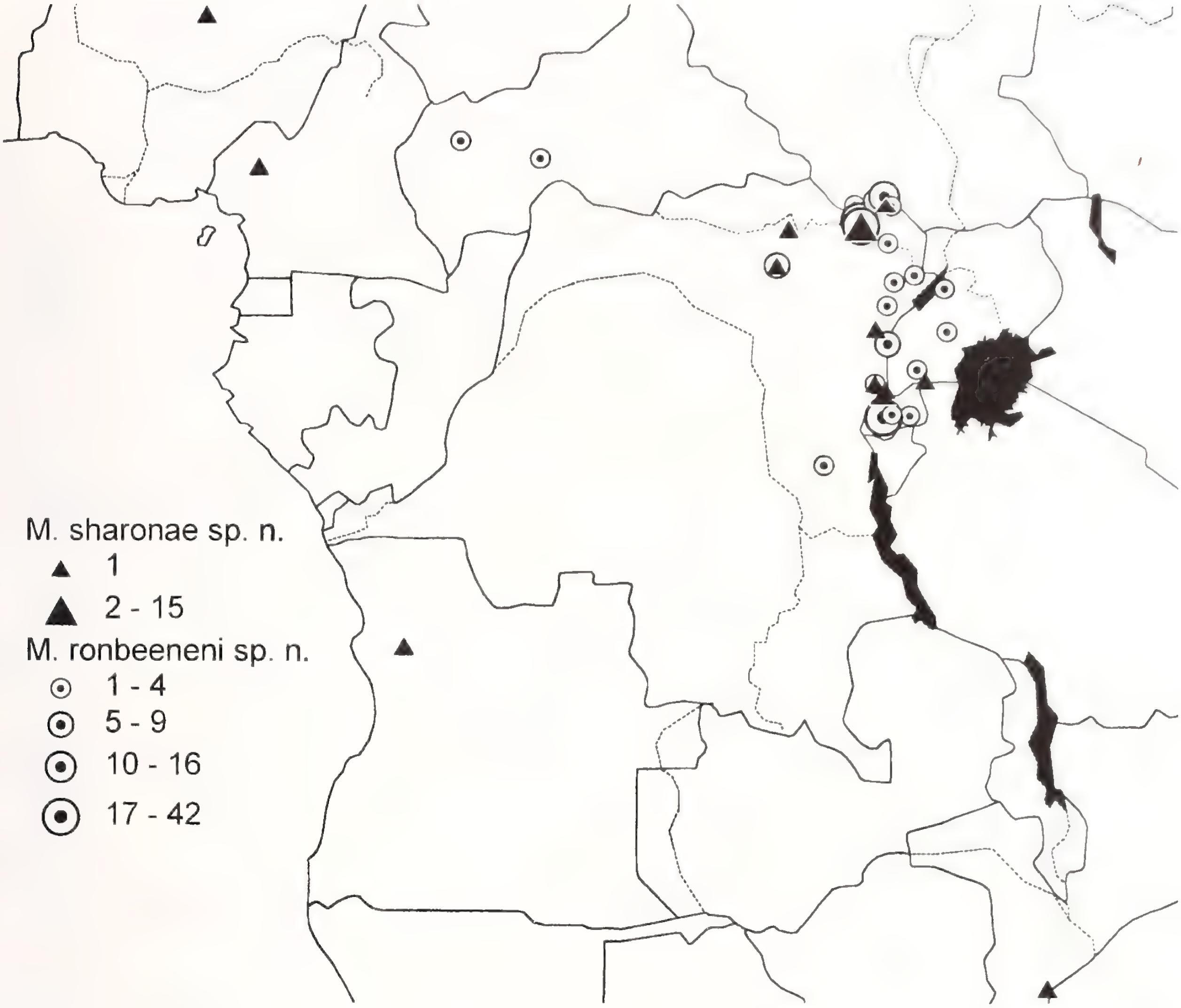


Fig. 32: Distribution of *Monolepta ronbeeneni* sp. n., and *M. sharonae* sp. n.

can be distinguished by more slender antennae and different elytral coloration.

Etymology. Dedicated to the Chrysomelidologist Ron Beenen, Nieuwegein, The Netherlands.

Type material.

Holotype: ♂ “Congo Belge, P.N.G., Aka, 19.V.1952, H. de Saeger, 3484” (MRAC); type locality: Congo, Parc National d’Garamba, 3.40N/29.00E.

Paratypes: **Central African Republic:** 1 ex., Dar-Banda, Merid., Krébédjé, Fort Sibut, 5.46N/19.06E, Miss. Chari-Tchad, X.1904, J. Decorse (MNHN); 1 ex., Uamgebiet, Bosum, 6.19N/16.38E, VI.1914, Tessmann (ZMHB). – **Congo:** 2ex., Ituri, La Moto, Madyu, 2,27N/26.25E, l. Burgeon (MRAC); 1 ex., Viag. Ruwenzori, S. A. R. D. Abruzzi (MIZT); 5 ex., Haut-Uelé, Moto, 2.27N/26.25E, 1920, V.1923, L. Burgeon (MRAC); 3 ex., Haut-Uelé, Abimva, 3.09N/29.50E, V.1925, L. Burgeon (MRAC); 2 ex., alto Uelle, Yakuluku, 4,20N/28.48E, IV.1927, F. S. Patrizi (MCSN); 4 ex., alto Uelle, Kapili, 3.42S/27.53E, V.1927, F. S. Patrizi (MCSN); 1 ex., Ituri, Nioka, 2.10N/30.39E, VI.1934, J. V. Leroy (MRAC); 2 ex. Rutshuru, 1.11S/29.27E, XII.1937, J. Ghesquière (MRAC); 1 ex., Mongbwalu, 1.57N/30.02E, VII.1938, Scheitz (MRAC); P.N.Garamba, 3.40N/29.00E: 1 ex., I/a/3, II.1950, H. de Saeger (MRAC); 2 ex., Akam, V.1950, H. de Saeger (IRSNB, MRAC); 4 ex., I/o/1 & I/o 2, V.1950, H. de Saeger (MRAC); 1 ex., km 31, V.1950, H. de Saeger (MRAC); 11 ex., I/o/1 & I/o/2, X.1950, Miss. H. de Saeger, G. Demoulin (MRAC); 2 ex., II/gd/9, XI.1951, H. de Saeger (MRAC); 4 ex., Garamba/2, source, VI.1952, H. de Saeger (MRAC); 1 ex., PFSK, 22/8, VI.1952, H. de Saeger (MRAC); 1 ex., PFNK, 12/9, VII.1952, H. de Saeger (MRAC); 1 ex., Mabanga, 4.22N/29.47E, II.1952, H. de Saeger (IRSNB); 8 ex., Pidigala, 4.27N/29.28E, IV.1952, H. de Saeger (1 IRSNB, 7 MRAC); 1 ex., Mt. Embe, 4.40N 29.33E, IV.1952, H. de Saeger (MRAC); 42 ex., Aka2, 3.50N 28.57E, V.1952, H. de Saeger (12 ex. IRSNB, 30 ex. MRAC); 16 ex., Inimvua, 4.35N/29.43E, V.1952, H. de Saeger (2 ex., IRSNB, 14 ex. MRAC); 1 ex., Iso, 4.18N/29.56E, III, IX.1952, H. de Saeger (MRAC); 1 ex., Mt. Moyo, 1.13N/29.49E, IX.1952, H. de Saeger (MRAC); P.N.A., Massif Ruwenzori, 0.20N/29.50E: 1 ex., Kyandolire, 1700 m, X.1952, P. Vanschuytbroeck (MRAC); 5 ex., Mt. Degio, 2200 m, VII.1954, P Vanschuytbroeck & H. Synave (MRAC); 1 ex., Litongo, 1575 m, VII.1954, P. Vanschuytbroeck (MRAC); 1 ex., Kombo, 1550 m, (MRAC); 1 ex., Kombo, 1550 m, VII.1954, P. Vanschuytbroeck (MRAC); 1 ex., Secteur Nord, Muramba, 1050 m, XI.1956, P. Vanschuytbroeck (MRAC); 1 ex., Katibombo, camp des gardes, 900 m, X.1957, P. Vanschuytbroeck (MRAC). – **Rwanda:** 1 ex., Kibungu, 2.10S/30.32E, X.–XII.1937, R. Verhulst (MRAC); 30 ex., Rubona, 2.13S/29.43E, "s/haricots", X.1966, I.S.A.R. (MRAC); 1 ex., Rubona, V.1963, G. Pierrard (MRAC); 2 ex., Icyanya, X.1972, coll. Roggeman (CBe); 4 ex., Mayaga, 2.06S/29.59E, V.1973, coll. Roggeman (CBe). – **Tanzania:** 1 ex., Mujenje, VIII.1913, Kittenberger (ZMHB). – **Uganda:** 1 ex., Koki Country, SW Buddu, 0.25S/31.40E, 4100 ft, X.1911, S. A. Neave (BMNH); 1 ex., SE Ankole, 0.45S/30.45E, 4400–400 ft, X.1911, S. A. Neave (BMNH); 1 ex., Kalwa, IX.1932, T. Jackson (BMNH); 1 ex., Budongo, 1.45N/31.35E, IX.1932, T. Jackson (BMNH); 1 ex., Kawanda, II.–III.1958, at light trap, P. Whalley (BMNH).

Monolepta sharonae sp. n.

Description.

Total length. 3.40–4.20 mm (mean: 3.75 mm; n = 8).

Head. Including mouth parts pale red to yellowish-red, with deeply incised transverse post antennal suture (Fig. 33). Antennae pale yellow, usually only tip of last antennomere dark brown, antennomeres 4 to 10 short, less than 4 times long than broad at apex. Length of antennomeres two to three 0.85–0.95 (mean: 0.90), length of antennomeres three to four 0.43–0.50 (mean: 0.47) (Fig. 34).

Thorax. Prothorax entirely pale yellow. Pronotal width 1.00–1.15 mm (mean: 1.08 mm), pronotal length to width 0.60–0.63 (mean: 0.61), finely punctured, pronotum usually significantly narrowed at base. Anterior quarter of elytra black, transverse black spots in the apical third of each elytron (Fig. 33). Elytral length 2.70–3.20 mm (mean: 2.85 mm), maximal width of both elytra 1.80–2.15 mm (mean: 2.04 mm), maximal width of both elytra to length of elytron 0.68–0.73 (mean: 0.71). Scutellum yellowish-red. Meso- and metathorax, coxa, trochanter an basal two third of femur reddish-yellow, outer parts of legs yellow.

Abdomen. Pale yellow.

Female genitalia. Spermatheca small, with small nodulus, slender middle part and slender cornu (Fig. 35). Dorsal part of bursa sclerites broad at base strongly narrowed towards apex (Fig. 36a), ventral part slender, outer margin finely serrate (Fig. 36b).

Male genitalia. Apical part of median lobe strongly narrowed, conical and dorsally bent towards apex (Fig. 37a), basal three quarter broad, parallel-sided (Fig. 37b). Tectum very broad, ventral groove of median lobe wide, narrowed towards the orifice (Fig. 37c). One median endophallic spiculum large and usually bent towards the right in dorsal view, another rpart of median spiculae short and twisted, ventral spiculae strongly bent, lateral spiculae complex curved, with strong, medially oriented spine at apex (Fig. 37b).

Distribution. This species is known from Nigeria through the Congo Basin to western Uganda and Rwanda, southwards to Central Moçambique and Angola (Fig. 32) and can be expected also in Rwanda, western Tanzania and Zambia.

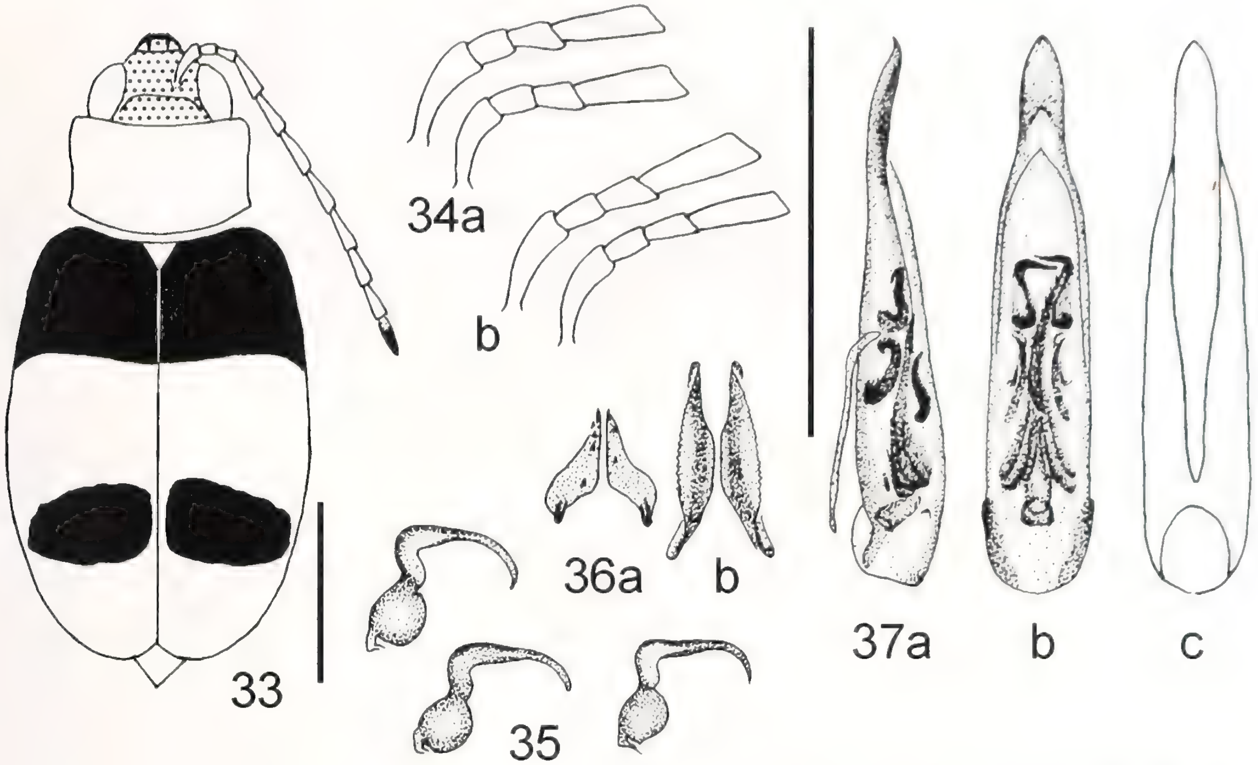
Diagnosis. *Monolepta sharonae* sp. n. is very similar to specimens of *M. vincta*, which has the same coloration type (Fig. 18c). Since it is sympatrically distributed with the very polymorphic *M. vincta*, both species can be clearly distinguished by examination of the male genitalia only (Figs 24, 24, 25, 37), while doubtless identification of females is not possible. *M. sharonae* sp. n. is on average smaller (total length up to 4.2 mm, *M. vincta* up to 4.7 mm), the basal antennomeres are longer (antennomere 3 to 4: 0.43–0.50, *M. vincta*: 0.28–0.37), and the post antennal suture is deeply incised in all known specimens of *M. sharonae* sp. n., but rarely found in *M. vincta*. Since only about ten percent of all available males of both species were examined in this study, there might be some more specimens of the new species beyond the material identified as *M. vincta*.

Etymology. Dedicated to the Chrysomelidologist Sharon Shute, The Natural History Museum, London, UK.

Type material.

Holotype. ♂ "Angola, (A26), Salazar, I.I.A.A., 9.-15.iii.1972 / at light / Southern African Exp. B. M. 1772-I" (BMNH); 9.18S/14.55E

Paratypes. **Cameroon:** 1 ex., Bafoussam, 5.31N/10.25E, II.1969, N. Berti (MNHN). – **Congo:** 1 ex., Ituri, La Moto, Madyu, 2.27N/26.25E, L. Burgeon (MRAC); 1 ex., Beni à Lesse, 0.30N/29.28E, VII.1911, Dr. Murtula (MRAC); 1 ex., Amadi, 3.35N/26.47E, IV.1913, P. van den Plas (MRAC); 1 ex., Rutshuru, 1.11S/29.27E, V.1937, J. Ghesquière (MRAC); 1 ex., P. N. Garamba, 3.40N/29.00E, I/o, V.1950, H. de Saeger (MRAC); 1 ex., P. N. Garamba, I/c, VIII.1950, G. Demoulin (MRAC); 1ex., P. N. Garamba, I/o/2, X.1950, H. de Saeger (MRAC); 2 ex., P. N. Garamba, II/gd, V.1951, H. de Saeger (MRAC); 3 ex., P. N. Garamba, PpK/60/d, XII.1951, H. de Saeger (MRAC); 2 ex., P. N. Garamba, II/fd, XII.1951, H. de Saeger (MRAC); 1 ex., P. N. Garamba, Tori, III.1952, H. de Saeger (MRAC); 1 ex., P. N. Garamba, Ndelele, 4.22N/29.47E, VI.1952, H. de Saeger (MRAC); 1 ex., P. N. Garamba, PFSK, VI.1952, H. de Saeger (MRAC); 1 ex., P. N. Garamba, Anie, VII.1952, H. de Saeger (MRAC); 2 ex., P. N. Garamba, II/jd/9, I., VIII.1952, H. de Saeger (MRAC). – **Moçambique:** 1 ex., Beira, 19.49S/34.52E, VI.1900, G. A. K. Marshall (BMNH). – **Nigeria:** 1 ex., Yengre, 10.14N/8.48E, VIII.1973, R. Linnavuori (MZHF). – **Rwanda:** 1 ex., Ruhengeri, source Kirii, 1.35S/29.40E, 1800–1825 m, X.1934, G. F. de Witte (MRAC); 1 ex., Kagogo, 1.22S/29.46E, 1990 m, I.1953, P. Basilewsky (MRAC). – **Uganda:** 1 ex., Daro Forest, Toro, 1.05S/31.00E, 4000–4500 ft, X.1911, S. A. Neave (BMNH).



Figs 33–37: *Monolepta sharonae* sp. n. 33: colour pattern; 34: basal antennal articles (a: ♂, b: .); 35: three different spermathecae; 36: bursa-sclerites (a: dorsal, b: ventral); 37: median lobe (a: lateral, b: dorsal, c: ventral, without endophallic structures).

***Monolepta naumanni* sp. n.**

Description.

Total length: 3.60–4.80 mm (mean: 4.23 mm; n = 10).

Head. Yellow, some specimens with pale brownish vertex (Fig. 38b), labrum, mandibles, maxillary and labial palpi brown. Antennae yellow, usually only last antennomere brown, rarely last two to three antennomeres brown (Fig. 38c). Antennae long, antennomeres 4 to 10 slender, elongate. Length of antennomeres two to three 1.00–1.05 (mean: 1.01), length of antennomeres three to four 0.37–0.43 (mean: 0.39).

Thorax. Prothorax entirely pale yellow. Pronotal width 1.10–1.45 mm (mean: 1.26 mm), pronotal length to width 0.58–0.61 (mean: 0.59), very finely and irregularly punctured. Anterior third of elytra black or dark brown, in 20 % of specimens examined reddish brown, middle pale brownish-yellow, each elytron with black (10 %; Fig. 38b), brown (70 %; Fig. 38c) or without (20 %; Fig. 38a) subapical spot, this spot with reddish outer margins (Figs Figs 38b, c). Elytral length 2.80–3.50 mm (mean: 3.18 mm), maximal width of both elytra 1.90 2.50 mm (mean: 2.31 mm), maximal width of both elytra to length of elytron 0.71–0.75 (mean: 0.73). Scutellum yellow or yellowish-red. Meso- and metathorax and legs brownish-yellow, apex of femur, tibia and tarsi paler yellow.

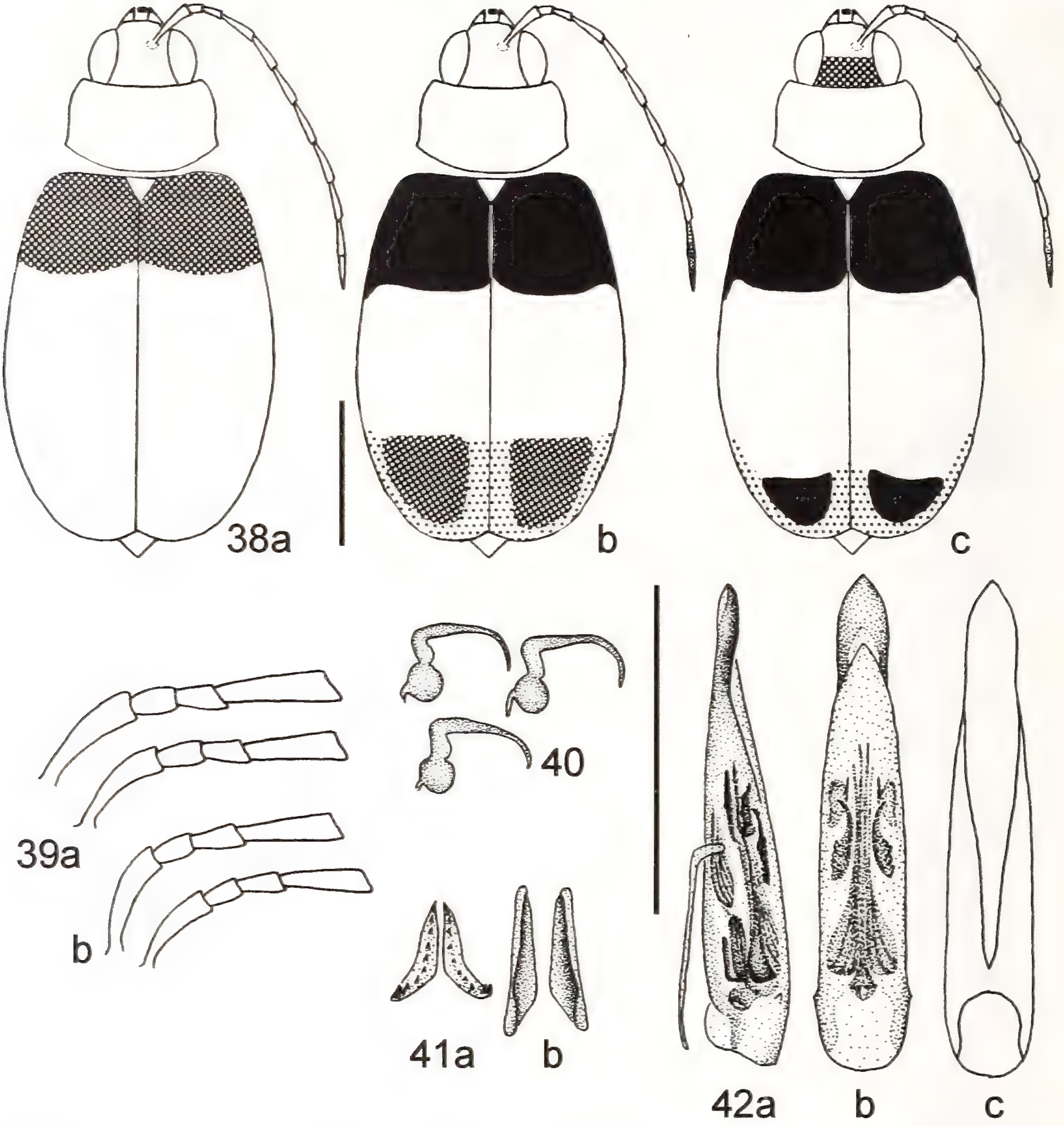
Abdomen. Brownish-yellow.

Female genitalia. Spermatheca small, with small nodulus, slender middle part and long and slender cornu (Fig. 40). Dorsal part of bursa sclerites slender, with small spines (Fig. 41a), ventral part slender, outer margin finely serrate (Fig. 41b).

Male genitalia. Apical part of median lobe narrow, conical towards apex, basal three quarter parallel-sided (Fig. 42). Tectum broad, conical (Fig. 42b), ventral groove of median lobe wide, strongly narrowed towards the orifice (Fig. 42c). Median endophallic spiculae slender, ventral spiculae strong, hook-like, lateral spiculae broad, short, plate-like medially with spur (Fig. 42b).

Distribution. Known from wet tropical forests from eastern Congo and Rwanda to southern Uganda, Western Kenya (Kakamega Forest) and north-west Tanzania (Ukerewe Island in Lake Victoria; Fig. 17).

Diagnosis. *Monolepta naumanni* sp. n. can be distinguished from all other species of the *Monolepta vincta*-group by the elytral coloration where subapical elytral spots have red outer margins. A very similar coloration is found in some specimens of *M. quadrizonata* Laboissière, 1940, which occurs syntopely with *M. naumanni* sp. n. at some locations, but is much larger (total length 5.50–6.40 mm), elytra are very slender, and genital characters of both sexes are very different (WAGNER



Figs 38–42: *Monolepta naumanni* sp. n. 38: colour pattern; 39: basal antennal articles (a: ♂, b: ♀); 40: three different spermathecae; 41: bursa-sclerites (a: dorsal, b: ventral); 42: median lobe (a: lateral, b: dorsal, c: ventral, without endophallic structures).

2003b). Specimens without apical spot and reddish-brown elytral base are very similar to some *M. umbrobasalis* Laboissière, 1940, which also occurs syntopely with *M. naumanni* sp. n. along the Albertine Rift and is very similar in size (total length, 3.30–4.10 mm) and external characters, but has very different genital characters including a broad and apically depressed median lobe (WAGNER 2002).

Etymology. Dedicated to the late Clas Michael Naumann, my unforgotten mentor.

Type material.

Holotype: ♂ "Uganda, District Masindi, Budongo Forest n. Sonso, 1°45'N, 31°35'E, 1.–10.VII.95, Th. Wagner leg. / T.r. 15 / 2" (ZFMK)

Paratypes: **Congo:** 1 ex., Malela, 4.22S/26.08E, XII.1913, L. Burgeon (MRAC); 1 ex., Alto Uelle, fl. Ouru, 2.07N/31.14E, II.1927, F. S. Patrizi (MCSN); 1 ex., Mongbwalu, Kilo, 1.49N/30.06E, 1938, Mme Scheitz (MRAC); 1 ex., Stanleyville, Ongoka, riv. Lowa, 1.23S/26.02E, IV.-IX.1952, J. Pantos (MRAC); 1 ex., P. N. Garamba, Mt. Embe, 4.40N/29.33E, IV.1952, H. de Saeger (MRAC); 4

(MRAC); 4 ex., P. N. Garamba, Aka, 3.50N/28.57E, V.1952, H. de Saeger (MRAC); 3 ex., P. N. Garamba, Dedegwa, 4.35N/29.43E, IV., V.1952, H. de Saeger (MRAC); 1 ex., Kivu Sud, Irangi, 1.54S/28.27E, 900 m, X.1993, insecticidal tree fogging of *Carapa grandiflora* (Meliaceae), Th. Wagner (ZFMK). – **Kenya:** 8 ex., Kakamega Forest near Buyangu, 0.18N/34.53E, IX.2001, X.2002, some by insecticidal tree fogging of *Teclea nobilis*, Th. Wagner (ZFMK). – **Rwanda:** 1 ex., Gisakura,2.00S/29.50E, VI.1972, coll. Roggeman (CBe). – **Tanzania:** 14 ex., Ukerewe Island, 2.09S/32.52E, ex. coll. Conrads (NMK). – **Uganda:** 2 ex., Kampala, 0.19N/32.35E, VI.1940, A. F. J. Gedye (BMNH); 1 ex., Kibale Forest, 0.50N/31.06E, 1983, M. Nummelin (MZHF); 4 ex., same label as holotype, insecticidal fogging of *Trichilia rubescens* (Meliaceae) and *Cynometra alexandri* (Caesalpiniaceae) (ZFMK); 2 ex., Semliki Forest, 0.48N/30.08E, II.1997, Th. Wagner (ZFMK).

Key to species

Afrotropical *Monolepta*-species, which are characterized by a black transverse band at the elytral base, a further transverse band or isolated black spots in the apical third of elytra, where other parts of elytra are yellow or yellowish-red, can be distinguished after the following key. It can be used for specimens up to 5.60 mm total length. Larger specimens (up to 6.70 mm) with the colour pattern mentioned above belong to *M. quadrizonata* Laboissière, 1940, which was revised elsewhere (WAGNER 2003b). Excluded from this key are also *Monolepta*-species which have a mid-elytral transverse black band, black outer elytral margins and often a red elytral suture like the abundant and widely distributed *M. elegans* Chevrolat 1837, *M. vinosa* Gerstaecker, 1871, *M. cruciata* Guerin-Menéville, 1858, and some other species, which will be revised in the near future.

1 Pronotum very broad (prontal length to width: 0.54–0.58; Fig. 7); second antennomere particularly in males very short (length of second to third antennomere: 1.00–1.40, length of third to fourth antennomere: 0.20–0.36; Fig. 8); small (total length: 3.00–4.20 mm); spermatheca of peculiar shape (Fig. 9); apical half of median lobe very slender (Fig. 11); known from savannas of West Africa towards north-eastern Congo .... ***Monolepta buquetii* Chevrolat, 1837**

– Pronotum less broad (prontal length to width: 0.58–0.67); second antennomere more elongated (length of second to third antennomere: 0.75–1.10, length of third to fourth antennomere: 0.28–0.62); often larger than 4.20 mm; spermatheca of different shape; median lobe less narrowed in the apical half, exceptions are M. ronbeeneni sp. n. and very few specimens of M. vincta, which differ in endophallic armature (Figs 25, 31) 2

2 Basal antennomeres elongated and slender, second antennomere of same length or longer than third (length of second to third antennomere: 1.00–1.10, Figs 28, 39); elytra usually with large isolated spot in the apical third, instead of a transverse band, other parts of elytra more reddish-yellow (Figs 27, 38); restricted to Guineo-Congolian forests in northern Central and western East Africa (Figs 17, 32) 3

– Basal antennomeres less elongated, second antennomere same length or shorter than third (length of second to third antennomere: 0.75–1.00, Figs 2, 13, 19, 34); elytra either with smaller isolated spot or transverse band in the apical third (Figs 1, 12, 16, 33), other parts pale yellow to yellow; distributed throughout tropical Africa; check of male genitalic structures is necessary in most specimens to ensure a correct identification, single females can sometimes not be allocated to species without doubt 4

3 Very small (total length: 3.10–3.60 mm); elytra slender (width of both elytra to length of elytron: 0.59–0.64, Fig. 27); third antennomere very long (length of third to fourth antennomere: 0.41–0.62, Fig. 28); Central African Republic towards western Uganda and Rwanda (Fig. 17) .... ***Monolepta ronbeeneni* sp. n.**

– Larger (total length: 3.60–4.80 mm); elytra broad (width of both elytra to length of elytron: 0.71–0.75, Fig. 38); third antennomere less elongated (length of third to fourth antennomere: 0.37–0.43); known from north-eastern Congo towards western Kenya (Kakamega Forest), Rwanda and north-western Tanzania (Ukerewe Island) .... ***Monolepta naumanni* sp. n.**

4 Third antennomere significantly longer than second (length of second to third antennomere: 0.75–0.88, Fig. 13), and about half as long as fourth antennomere (length of third to fourth antennomere: 0.46–0.54); pronotum comparatively slender (prontal length to width: 0.63–0.67); known from Eritrea, northern Somalia, Arabian Peninsula, Israel and Jordan (Fig. 17) .... ***Monolepta lepida* Reiche, 1858**

– Third antennomere shorter (length of second to third antennomere: 0.86–1.00; length of third to fourth antennomere: 0.30–0.50); pronotum broader (prontal length to width: 0.58–0.65); tropical Africa only 5

5 On average larger (total length: 3.80–5.60 mm); median lobe homogeneously conical and slightly widened at apex (Fig. 5); north-eastern Congo and Uganda towards the Cape, most abundant and widely distributed in southern Africa (Fig. 6); specimens which occur syntopely with M. vincta are significantely larger than those.......................... ...... ***Monolepta melanogaster* (Wiedemann, 1823)**

– On average smaller (total length: 3.25–4.75 mm); median lobe narrowed and parallel-sided at apex (Figs 23, 24, 37); throughout tropical Africa but not known from the Republic of South Africa, and rare in other countzries of southern Africa 6

6 Third antennomere more elongated (length of third to fourth antennomere: 0.43–0.50, Fig. 34); transverse post antennal suture deeply incised, pronotum pale yellow (Fig. 33); lateral endophallic spiculae strong, curved inwards, hooked at apex (Fig. 37); Nigeria through Congo basin towards western Tanzania, Zambia......... ***Monolepta sharonae* sp. n.**

– Third antennomere shorter (length of third to fourth antennomere: 0.28–0.37, Fig. 19); transverse post antennal suture usually not incised, pronotum often red, rarely black; endophallic armature different (Figs 23, 24, 25); throughout tropical Africa with exception of South Africa
.... ***Monolepta vincta* Gerstaecker, 1871**

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Bonner zoologische Beiträge | Band 53 (2004) | Heft 1/2 | Seiten 283–289 | Bonn, Juni 200

Diversity Patterns of Plants and Phytophagous Beetles in Sub-Saharan Africa[1]

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Abstract. Species distribution of flowering plants (Angiospermae) and the phytophagous beetle group *Monolepta* (Chrysomelidae) in Sub-Saharan Africa (south of 17° N) are compared based on species numbers per square degree grid. The beetle data comprise all 89 valid species for Africa (21,000 specimens of Afrotropical *Monolepta* have been currently revised). The plant diversity data are based on 6,269 species with some 330,000 distributional records (10–15 % of all African angiosperm species). Shared centres of species richness of both taxa are geodiverse, montane forests, namely the Albertine Rift, Eastern Arc Mountains, isolated East African volcanoes, montane areas in Cameroon and northeastern parts of a the Republic of South Africa. However, the Cape and the Upper Guinea Region show diverging patterns: plant species richness is higher than the richness of Chrysomelidae. Actual diversity patterns versus sampling artefacts are discussed. Certain mechanisms, like allopatric speciation processes, contribute to a diverse flora and fauna in areas of high geodiversity. Thus, if there is a general and taxon-independent positive relationship between geodiversity and species richness, these areas are of explicit value for the conservation of terrestrial biodiversity.

Key words. Angiosperms, Chrysomelidae, biodiversity, biogeography, distribution patterns, conservation

1. Introduction

The understanding of the spatial distribution of biodiversity is a fundamental requirement for its conservation and sustainable use. However, current biogeographic knowledge is restricted to a tiny proportion of terrestrial biodiversity. While there is comparatively detailed information on the global distribution of vertebrate diversity (RODRIGUEZ et al. 2004), there is only little information about the spatial distribution of the remaining 99 % of animal species, particularly for such a megadiverse group like insects. More problematic, the representativeness of patterns of vertebrate diversity, e.g. patterns of insects, might be limited. In contrast, plants in their function as the foundation of food-webs may serve as a surrogate to assess patterns of overall terrestrial biodiversity (BARTHLOTT et al. 1996, 1999).

Flowering plants and beetles, in particular the most speciose phytophagous beetle taxa, Chrysomeloidea and Curculionoidea, represent one of the oldest and largest radiation of plant-animal co-evolution (FARRELL 1998). The diversity of flowering plants (BARTHLOTT et al. 1996, 1999) and the extent to which phytophagous beetles are specialized on their food-plants, were the basis for estimations which dramatically changed our idea of terrestrial biodiversity (ERWIN 1982). Despite the extend of specialisation of phytophagous beetles in tropical biomes and that numbers have been clearly overestimated on the basis of conclusions from temperate regions (MAY 1990; ØDEGAARD 2000; WAGNER 2000a; NOVOTNY et al. 2002), there is no doubt that the number of existing species is several times higher than the number of yet described species. This is particularly true for the approximately 150,000 species of leaf beetles and weevils (LAWRENCE & BRITTON 1991).

Both beetle groups illustrate the most prominent problem of biodiversity research. The more speciose taxa are and the smaller the mean range size of their species is, the less complete is our knowledge on their large scale biogeographic patterns. While the global distribution patterns; e.g. of the vertebrates, which have on average a large range size, are apparently known on a 0.5° degree resolution (RODRIGUES et al. 2004), the situation for plants (SCHATZ 2002) and particularly arthropods is completely different. While plants are at least relatively well known from a taxonomic perspective, there is a strong need for taxonomic research on arthropods. This includes the phytophagous beetles, which have an key ecological position in the food-web as the most species rich group of first order consumers. Thus, chrysomelids provide a good example for studying speciation processes, including co-evolution of angiosperms and their consumers in tropical systems.

Since a detailed assessment of arthropod diversity patterns at the global scale is impossible, we rely on data for selected groups and selected areas. Based on the most comprehensive databases on the Sub-Saharan distributions of plants and the chrysomelid group of *Monolepta*, we exemplarily compare centres of species richness of plants and phytophagous beetles. We discuss consequences of the quality of available biogeographic data for our knowledge on the biodiversity of both groups and for potential application of these data for conservation biology.

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[1] In commemoration of Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004)

2. DATA AND METHODS

2.1. Taxonomy and diversity data for *Monolepta* (Chrysomelidae)

Afrotropical species of *Monolepta* Chevrolat, 1837 were recently revised (WAGNER 2003a). These beetles form the largest group of the Galerucinae (Chrysomelidae), having worldwide about 600 nominal species. Many of the 160 species described from Africa were found to be synonyms or needed to be transferred to other genera due to their phylogenetic position. However, 50 valid species remained in *Monolepta*, and there is about the same number of new species, most of them presently described (WAGNER 2000b, 2001b, 2002, 2003b; Wagner this issue) or awaiting description. Unfortunately, food-plants of most *Monolepta* species are still unknown. There are only very few data available from labels of dried specimens, with direct observations in the field and literature (JOLIVET & HAWKESWOOD 1995) indicating that some species feed on *Citrus* sp. and some others on other Rutaceae. The revision of the 89 valid species of Afrotropical *Monolepta* is based on 21,000 specimens. Five hundred specimens are recently collected mainly in eastern Africa, while most are dried specimens from all major collections housing African insects, principally museums in Berlin, Brussels, London, Nairobi, Paris, Pretoria, Tervuren and Windhoek.

After this comprehensive revision of material, detailed data on the distribution of Afrotropical *Monolepta* species are now available. Only four *Monolepta* species are distributed throughout tropical Africa, and known from a variety of biomes such as tropical forests, savannas and even deserts, from coastal regions to montane areas. All other species show more restricted geographical and ecological distributions. Forest-dwelling species are often more restricted and a high degree of endemism is found amongst species from montane areas (WAGNER 2001a). Coordinates are derived from label data on distribution using a gazetteer compiled by Ugo Dall'Asta (Africa-Museum, Tervuren) for locations from Congo (Zaire) and generally using the Alexandria Digital Library Gazetteer Server. Data of all *Monolepta* species is based on 2320 localities in subsaharan Africa.

2.2. Diversity data for Plants

Earlier versions of the plant dataset have been described and analysed in previous publications (LINDER 2001; LOVETT et al. 2000; LINDER et al. 2005; KÜPER et al. 2004; Lovett et al. 2004). Since 2003, an international group of research institutions has contributed data on the distribution of African plants to the *Biogeographic Information System on African Plant Diversity,* which is hosted and curated by the BIOMAPS Project within the BIOLOG-BIOTA framework (www.biota-africa.org). The spatial precision of the distribution data varies between exact localities mainly from herbarium collections with georeferenced localities, to 1° resolution data from digitised maps. Additional information on the origin of this dataset is documented in BURGESS et al. (in press, see also Acknowledgements).

The current database covers African-wide distribution records for 6,269 species (status as of March 2004), all of which had been taxonomically revised. This comprises between 10 and 15 % of the African angiosperm species (LEBRUN & STORK 1991–1997; BEENTJE et al. 1994). There are currently 330,000 distribution records in the form of confirmed collection localities available.

2.3. Data preprocessing and analysis

Data are organized in MS Access databases and have been plotted and analysed using ArcView 3.2a GIS software. In order to achieve maximum comparability with previous analyses on Sub-Saharan diversity (BALMFORD et al. 2001; BROOKS et al. 2001; BURGESS et al. 2002, in press; DE KLERK et al. 2004), all distribution data were rescaled to a 1° grid resolution within a base map of 1,713 one-degree latitude-longitude grid cells covering mainland Sub-Saharan Africa south of 17° North. By restricting the geographic coverage to Africa south of the Sahara and excluding those species only found on offshore islands, a database with 5,985 plant species and 89 species of *Monolepta* remains for further analyses. For the scatterplot, we only used those 580 grid cells in which at least one species of both groups occurred.

3. RESULTS

3.1. Shared centres of diversity of plants and *Monolepta*

There is an overlap of centres of high plant and *Monolepta* diversity in montane areas, namely the Albertine Rift system including the Virunga Volcanoes, the Ruwenzori, Bwindi Impenetrable Forest and the Kahuzi Biega National Park at the south-western extreme; the Eastern Arc, in particular East Usambara; the isolated East African Mountains such as Mt. Elgon, Mt. Kenya and Mt. Kilimanjaro; southern Katanga (Mitumba and Kundelungu Mountains, major collections in Upemba/ Kundelungu National Park and close to Lubumbashi); and to a lesser extend afromontane regions in Ethiopia, the northeastern parts of the Republic of South Africa, and lower Guinea (Fig. 1a/b).

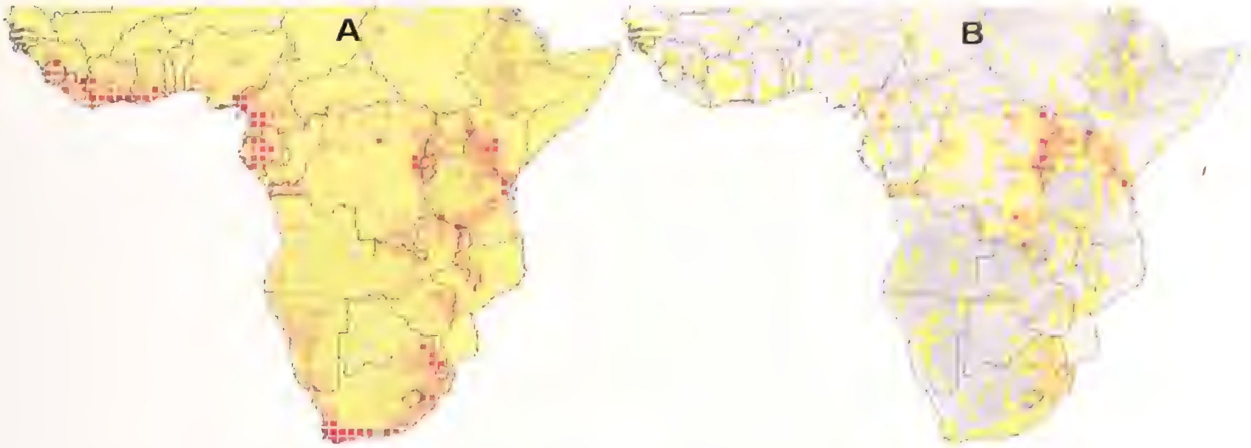

Fig. 1: Species richness per one-degree grid cell in Sub-Saharan Africa south of 18th degree latitude. – A. plants, n (species) = 5985, B. *Monolepta*, n (species) = 89). Richness values are rescaled to percentages of the maximum richness per grid of each taxon (*Monolepta*: max = 20; for plants: max = 682). The scale ranges from high species richness (dark red) to low species richness (bright yellow). In grid cells with no present species, the grey background colour represents elevation above sea level (dark grey: high elevation, bright grey: low elevation). Black foreground lines indicate national boundaries.

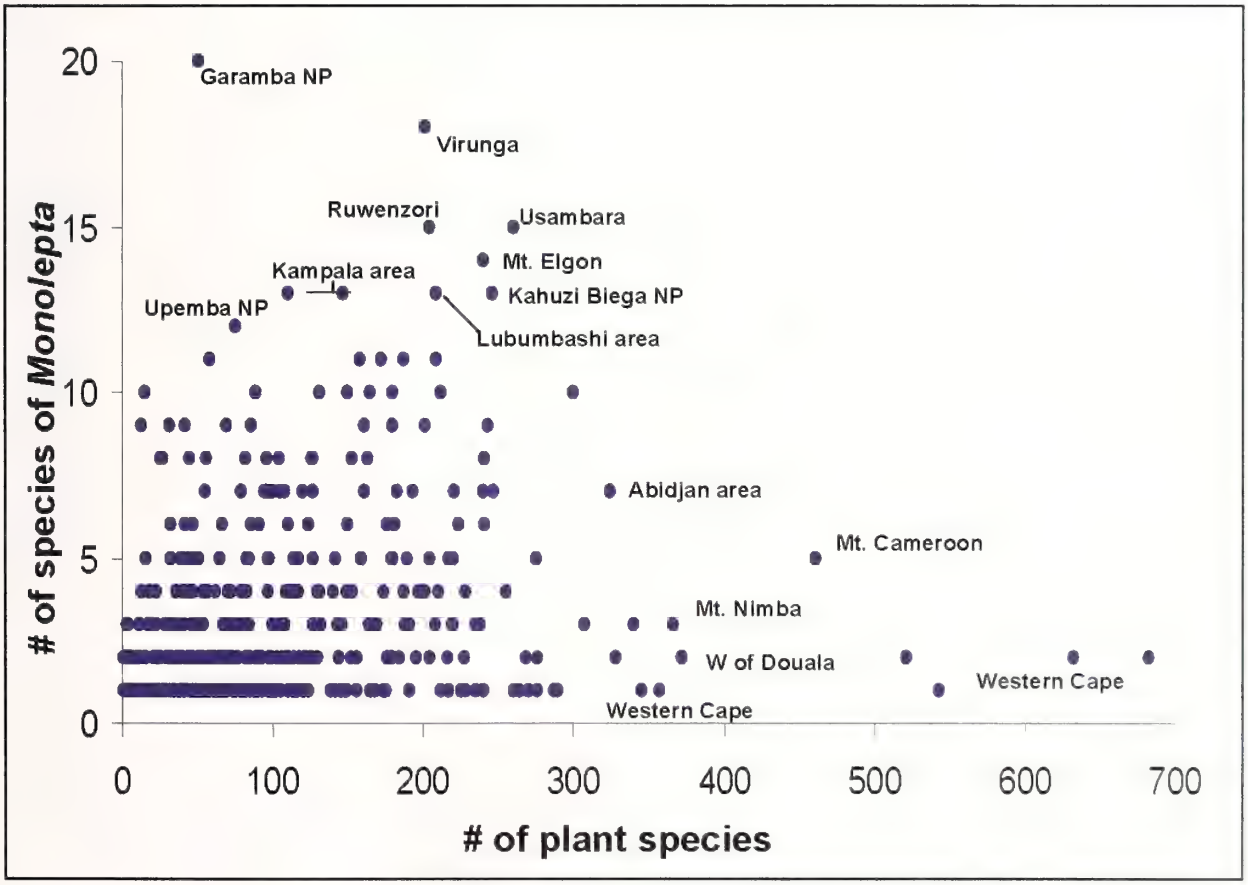

Fig. 2 : Species richness of *Monolepta* and plants in 580 one-degree grid cells in Sub-Saharan Africa. Only grids where both taxa were present with at least one species are considered. Outliers were labelled according to their geographic position (NP: National Park).

3.2. Divergent diversity patterns of plants and *Monolepta*

Even though some centres of species richness of both groups do coincide, the correlation between the patterns of species richness of plants and *Monolepta* are very low (Fig. 2). The correlation can probably be explained merely by the fact that the majority of the *Monolepta* species occur in forest habitats, and that forests are comparatively phytodiverse. The most obvious difference between the diversity patterns of plants and beetles is the outstanding plant diversity of the Cape Floristic Kingdom. This observation is contrary to all animal taxa yet mapped such as vertebrates (BROOKS et al. 2001) but apparently also insects (GILIOMEE 2003). There is no doubt that this pattern is based on ecological and historical characteristics of this landscape, which seem to favour certain plant taxa more strongly than any animal taxon. The same is true for the Succulent Karroo.

Few grids, all in regions with savannah habitats, have an exceptionally high number of *Monolepta* species, but comparatively low number of plant species. These are Garamba National Park in north-eastern Congo, Upemba National Park in south-eastern Congo (Katanga), the region west of Katanga along the Lulua River and the region around Kampala in Uganda. These areas belong to the best-collected regions for these beetles (and generally for insect groups). Some extended expeditions have been carried out in national parks in the former Belgian Congo over the years, and about 18 % of all known specimens of Afrotropical *Monolepta* are from Garamba National Park alone. Hence, high diversity in these particular grids is biased by high sampling effort. The Upper Guinea region, characterized by high plant diversity, has low beetle diversity. Since West Africa is less well sampled for *Monolepta* than all other African regions, this is most likely also a sampling artefact. However, this region lacks high mountains as typical for the rift systems in Central and East Africa, and *Monolepta* may be generally less diverse in West Africa.

Due to the strong influence of sampling intensity on the *Monolepta* dataset, there are no significant correlations of the derived species richness patterns of these beetles (or the residuals between the species richness of *Monolepta* and plants) with abiotic factors such as hydrothermic parameters (e.g. waterbalance, number of dry months), and topodiversity. Correlations between species richness of *Monolepta* and either plants or abiotic parameters did not improve when tested on the larger spatial scale.

4. DISCUSSION

4.1. Afrotropical Mountains: centres of biodiversity

On a global scale, many centres of plant diversity are located in tropical montane areas such as the South American Andes, the Eastern Arc, Crystal Mountains, Papua New Guinea, Himalaya or the Mesoamerican Cordillera Central (BARTHLOTT et al. 1999; MUTKE & BARTHLOTT 2005). In Africa, the montane regions Albertine Rift, the Eastern Arc, the Southern Rift extending into Chimanimani-Nyanga, the northeastern part of South Africa extending from Sekhukhuneland and Soutpansberg into the Maputaland Centre, and the West African Mt. Cameroon are well known centres of richness and endemism for a variety of ecologically very different taxa such as birds, mammals, snakes, amphibians (BROOKS et al. 2001) and plants (MUTKE et al. 2001).

Our study gives evidence that this also is the case for phytophagous beetles. Most *Monolepta* species in Central and East Africa have a restricted distribution. Twelve species are endemic to montane forests along the Albertine Rift, ten are restricted to East African mountains in Kenya and Tanzania, mainly to Mt. Kenya, Mt. Kilimanjaro and to the Eastern Arc Mountain mosaic, and a further nine species are restricted to montane areas in Ethiopia and Eritrea (WAGNER 2001a). To a lesser extent, montane regions in Cameroon also have higher species diversity and some endemic species. The diversification of many *Monolepta* species is obviously strongly effected by geographical speciation in isolated montane forests.

Many of the forest-dwelling *Monolepta* species appear to be young species in evolutionary terms. The Quaternary extension of the forest biome may be crucial in explaining the distribution pattern. In the late Pleistocene, the climate, particularly in central and East Africa was much cooler and drier (HAMILTON 1981). The timberline was about 1000 m lower than at present (e.g. BONNEFILLE et al. 1990; LOVETT 1993) and most lowland areas, including the Congo Basin, were too dry for forest vegetation and were covered by savannahs. The proposed forest refuge core areas coincides well with the highest degree of endemism and diversity of *Monolepta* in montane areas of Cameroon, the Albertine Rift and higher mountains in Kenya and Tanzania, including the Eastern Arc Mountain mosaic. Other *Monolepta* species, which are restricted to dry forest and savannahs, have a wider range. In the early Holocene, the climate became warmer and more humid. Wet tropical forests expanded to a presumed maximum about 6,000 years ago (HAMILTON 1981). During that time the Sudano-Zambesian savannah zone was presumably separated into a north-western and a south-eastern part, leading to a corresponding distribution pattern also found in other insects like butterflies and paussid beetles (CARCASSON 1964; NAGEL 1987).

Combined analyses on large scale biodiversity, in particular those comparing such different taxa like beetles and plants, have been heavily criticised as paradoxical, since they tend to neglect the diversity of ecological characteristics at the species level (HUSTON 2001). Indeed, the influence of abiotic factors or historical processes depends on the characteristics of each taxon. For example, steep topography or climatic fluctuations can lead to reduced gene flow between populations, but this strongly depends on the mobility of the animals or seed vagility in plants. The high degree of endemism in the Cape flora is partly interpreted as a consequence of the low dispersability of a high proportion of the species; e.g. of about 1000 ant-dispersed species in the Fabaceae, Proteaceae, Restionaceae, Rhamnaceae, and Rutaceae (GOLDBLATT & MANNING 2002). For the most speciose and endemic plant taxon in the South American Andes, the Orchidaceae, it is not dispersal but limited mobility of highly specialized arthropod pollinators that may be a key to understanding the extremely high number of local endemic species (KÜPER et al. 2004).

Nevertheless, if considering biodiversity not exclusively a result of the spatial distribution of abiotic factors (pattern diversity) but as a result of a variety of mechanisms (process diversity), it is clear that geodiverse, montane areas are an ideal place where a high variety of mechanisms in parallel can promote high levels of diversity: the steep orography can promote allopatric speciation processes, whereas orographic rainfall and horizontal mist interception in mountains may facilitate survival of species during long-term climate dynamics (FJELDSÅ & LOVETT 1997) and opportunistic colonialisation by widespread species. Habitat suitability but also habitat diversity as a consequence of geodiversity, provide suitable conditions for a speciose and structurally rich vegetation which in turn promotes consumer diversity due to diverse habitats and a high net primary production.

The afromontane areas, the Cape and parts of the West African upper Guinea Centre of plant diversity, cover more than 80 % of the Sub-Saharan flora on less than 10 % of its total area (KÜPER et al. 2004). Preliminary analyses suggest that the proportion of the Sub-Saharan vertebrate fauna covered by these areas might be even higher than that for plants (BROOKS et al. 2001), and the situation for phytophagous insects may be similar.

Due to the provided habitat diversity, one explanation for species richness of the Arotropical mountains might be the high number of overlapping ranges contributed by species of taxa which have their actual centre of diversity at different places. However, a significant number of endemic species and species with small distribution ranges of different taxa are restricted to Afrotropical mountains. The occurrence of similar diversity stimulating mechanisms in very different taxa highlights the importance of Afrotropical mountains as overall centres of terrestrial biodiversity.

4.2. Consequences of fragmentary biodiversity information

Our plant data are the most comprehensive ever assembled for the study area, but inevitably have limitations. There are certain areas in Ethiopia, the Sudan, the Central African Republic, the Republic of the Congo, the Democratic Republic of the Congo and Angola, whose plant diversity is not adequately documented (KÜPER, unpubl. data), and the scientific exploration of these areas is a most important challenge for the future. Unsurprisingly, the situation is even more problematic for phytophagous beetles. While the low diversity in Upper Guinea may be partly explained by the relative scarcity of montane areas; e.g., the Crystal Mountains in Gabon and Equatorial Guinea, are clearly undersampled. The concentration of the present records to urban areas or such with a comparatively good infrastructure (e.g. Addis Ababa, Mbandaka, and several National Parks) is symptomatic for sampling artefacts. Currently it is not possible to quantify how much of the congruence in richness patterns of beetles and plants in our database is due to the fact that the same areas tend to be better collected for both taxa, resulting in a comparatively high number of species of both groups in these cells.

The more speciose taxa are, and the smaller the mean range size of their species is, the less complete is our knowledge on their large scale biogeographic patterns. At the same time, the restricted knowledge concerning the distribution of any taxon limits its consideration in spatial priority setting approaches for nature conservation.

Current conservation approaches in Africa are mainly based on patterns of vertebrate diversity (BURGESS et al. 2004; FJELDSÅ et al. 2004; DE KLERK et al. 2004). This may mainly result from their charisma, making them attractive for funding as well as for non-scientific but valuable field survey by lay people, and also from the history of Africa's protected areas (FJELDSÅ et al. 2004). Whereas about 95 % of the vertebrates in Sub-Saharan Africa are covered by the existing set of IUCN protected areas, the proportion for plants covered by the same set is at 74 % (BURGESS et al. in press). Only in a few cases are large scale patterns of plant diversity more appropriately considered, e.g. for the Republic of South Africa (COWLING et al. 2003). Though an amount of about 140 million plant specimens have been collected globally (BGCI 6/2004), estimations on the basis of the TROPICOS database at the Missouri Botanical Garden revealed that for about 80 % of all taxa which are represented in the form of collections, there are less than ten collection localities worldwide (SCHATZ 2002).

A large attraction of currently available numerical algorithms for selecting conservation areas is that they can go beyond subjective preferences for the cute and the cuddly, but if biogeographic data and phylogenies are available only for "attractive" groups, we are no further forward (MACE et al. 2003). For arthropods, most likely less than 20 % of the existing species have been described so far. The risk of this situation is that we are actually considering only the tip of the iceberg of problems in nature conservation.

The bad message from our study is that even after spending several ten thousand hours of manpower on the collection of the distribution of African plant species and checking label data of about 21,000 beetle specimens, we are far from a satisfying documentation and understanding of the large-scale diversity patterns of these taxa.

The good news might be, if such different taxa like vertebrates, plants and phytophagous beetles do have centres of biodiversity in common, it may be possible to protect a large proportion of species, in relatively well defined and small areas. These areas possibly comprise species that are not yet described. Unfortunately, in many cases exactly these areas are also most attractive for human settling (CINCOTTA et al. 2000; BALMFORD et al. 2001). Hence, more comprehensive evidence showing taxon-crossing relevance of these areas could at least be a solid argument in favour of the sustainable use and protection of its biodiversity.

Ackowledgements. We thank the numerous experts who have assisted to compile the plant and beetle data used in this paper. The establishment and co-ordination of the Biogeographic Information System on African Plant Diversity at the Nees Institute for the Biodiversity of Plants in Bonn is funded by the German Federal Ministry of Education and Research (BMBF-BIOLOG Programme) and the Akademie der Wissenschaften und Literatur, Mainz. We thank Henk Beentje (Kew), Cyrille Chatelain and Laurent Gautier (Geneva), Tony Rebelo (Kirstenbosch), Jerome Degreef (Meise), Peter Frankenberg (Stuttgart), Norbert Jürgens (Hamburg), Don Kirkup (Kew), Sigrid Liede (Bayreuth), Peter Linder (Zürich), Roger Polhill (Kew), Adjima Thiombiano (Ouagadougou), Mauricio Velayos and Fernando Casas (Madrid), Jan Wieringa and Marc Sosef (Wageningen) and Georg Zizka (Frankfurt) for valuable contributions to the plant distribution dataset. We thank Henning Sommer for fruitful discussions and Jens Mutke for his efforts to establish and maintain the BIOMAPS working group in Bonn. Juliane Dame assisted with the manuscript.

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Bonner zoologische Beiträge

Herausgegeben vom

Zoologischen

Forschungsmuseum

Alexander Koenig,

Bonn

Band
53
Heft 3/4
2005 (2004)

Leibniz
Gemeinschaft

NRW.

Bonner zoologische Beiträge werden publiziert im Eigenverlag Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn (Germany)

Die Zeitschrift erscheint mit vier Heften im Jahr, zum Preis von 11,50 € je Heft bzw. 46,- € je Band incl. Versand. Korrespondenz betreffend Abonnement, Kauf oder Tausch bitten wir zu richten an die Bibliothek, Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn (Germany). E-mail: d.steinebach.zfmk@uni-bonn.de.

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ISSN 0006-7172

Druck: Druck Center Meckenheim

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Bonner zoologische Beiträge	Band 53 (2004)	Heft 3/4	Seiten 293–295	Bonn, Dec. 2005

Do Endings of Adjective Flectible Species Names Affect Stability? A Final Note on the Gender of *Podarcis* Wagler, 1830 (Reptilia, Lacertidae)

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Abstract. We here reply to the arguments put forward by Arnold (2000) and Lanza & Boscherini (2000) concerning the gender of the genus *Podarcis*. Arnold's argument that a change of endings of adjective flectible species names threatens stability is rejected by clearly following the articles of the current edition of the Code (ICZN 1999). We finally conclude that the gender of *Podarcis* must be masculine for the following reasons: (1) Wagler (1830) did not determine the gender by combination with any species name nor by statement, (2) the name *Podarcis* is of common variable gender, (3) the Principle of First Reviser does not apply to determination of gender of names, (4) the Code clearly states that a name of common variable gender is to be treated as masculine.

Key words. Grammatical gender, nomenclature, stability of names.

In a previous note, Böhme (1997) had argued that the lacertid lizard genus *Podarcis* was not of feminine (as generally used before) but of masculine gender. This view provoked strong criticism (Mayer 1998; Arnold 2000; Lanza & Boscherini 2000). Whereas Böhme (1998) replied already to the critics of Mayer (1998), we feel it also necessary to answer on the views put forward by Arnold (2000) and by Lanza & Boscherini (2000).

Böhme's (1997) main argument for the 'masculinization' of *Podarcis* was not the Homerian use of the Greek adjective podarkes attributed to the ancient hero Achilleus (*Αχίλλευς*); this circumstance was only a first hint to the problem, which lead to question the feminine gender of this lacertid genus name. The point was rather the assumption that Fitzinger (1843) was the first to fix a type species for *Podarcis* Wagler, 1830, viz. *Seps muralis* Laurenti, 1768. Furthermore, although being aware that *muralis* is again an ambiguous adjective as to its gender (masculine or feminine), Böhme (1997) regarded the genus name *Seps* in Laurenti's (1768) use as masculine because this author himself used it clearly in this way by describing for instance *Seps argus* and *Seps ruber* (= *Lacerta agilis* Linnaeus, 1758) in the same work. Laurenti's (1768) practice is apparent in other 18th century names, e.g. *Seps stellatus* Schrank, 1798 (likewise a synonym of *L. agilis*). Some 19th century names, however, implied *Seps* also to be a feminine noun, combining it with species names such as *Seps vittata* Leuckart, 1828 or *Seps quadrilineata* Metaxa, 1833, but this does not affect the original combination and therefore masculine determination of the genus' gender by Laurenti (1768). From these grounds, we think that the viewpoint to regard *Seps* Laurenti as masculine is still justified.

In contrast, Böhme's (1997) assumption that Fitzinger (1843) was the first to have 'masculinized' *Podarcis* Wagler by fixing a (masculine) type species, cannot withstand the arguments put forward by Arnold (2000) who justifiably states that *Podarcis* was earlier treated as feminine by Bonaparte (1836), since this author used the combinations *Podarcis taurica, P. oxycephala* and *P. muralis sicula* and conformed this usage subsequently (Bonaparte 1839).

However, the discussion about the first revising author according to article 24.2. (ICZN 1999) does not apply to the determination of gender of names, as already stated correctly by other authors (Kwet 2001, Caramaschi 2004). The Code does not allow the adscription of the gender by any subsequent author and all the sources for gender identification must be found in the original publication. Therefore, the arguments of Böhme (1997) and Arnold (2000) concerning first reviser's action are both not applicable to clarify the grammatical gender of *Podarcis*.

Lanza & Boscherini's (2000) arguments for a feminine gender, however, are very weak. They do restrict the problem to the philological "side of the medal". They regard Böhme's (1997) view an "unverifiable hypothesis", but assume instead that "almost surely the etymology of *Podarcis* is not from the Greek adjective 'podarkes' but from the Latin proper name Podarce (....), of course of Greek derivation, meaning 'Swiftfoot' and mentioned by Homer as one Harpy....". This assumption that Wagler's (1830) name *Podarcis* is not at all derived from an adjective, but from a "Latin proper name" (why should Homer use Latin names in his "Iliad"?) is likewise an unverifiable hypothesis and cannot be taken as "evidence" for a proposed continuing use of *Podarcis* as feminine.

We therefore agree with ARNOLD (2000) in that *Podarcis* derived from the Greek (subsequently Latinized) adjective "podarcis" with originally undetermined gender. We disagree, however, with ARNOLD's (2000) further reasoning that a change of a genus' gender and a subsequent adaptation of the endings of species names (as required by Article 34.2. of the Code) would "contravene the spirit of the International Code of Zoological Nomenclature (International Trust of Zoological Nomenclature, 1999) which promotes the stability of names, for example in the Preamble (p. 2) and in Articles 23.2 and 81)". Our point is here, that a change of the ending of an adjective flectible species name does not touch the problem of stability and universality at all. A changed ending of a given name is not a new or a different, but absolutely still the same – and therefore stable – name. We think that the change of an ending of a specific name as an adaptation to the gender of a changed, different genus should be regarded as a normal process, because the change of generic names is due to zoological arguments and thus has nothing to do with nomenclatural instability. A good and rather recent herpetological example is that of the spiny-tailed agamas, *Uromastyx,* a genus which was treated as masculine for decades until LANZA (1983) justifiably claimed that there is hardly a more feminine word to be found than the Greek word "mastix", wherefore *Uromastyx* is clearly and in a philologically correct way to be considered as feminine. No problems arose since then to change the naming of *Uromastyx acanthinurus, U. aegyptius, U. ocellatus, U. ornatus,* etc. into *U. acanthinura, U. aegyptia, U. ornata* and so on, just because the names have not at all been changed, and the "virtues of stability" (ARNOLD 2000) have been respected.

ARNOLD's (2000) further argument that the change of a species name's ending could cause confusion in non-specialist users is also not convincing to us. To stay with the example of *Uromastyx*, even non-taxonomist working in applied disciplines such as ecology, etc. could not really suspect *U. loricata* to be a different taxon from *U. loricatus*. A similar case (out of hundreds more) is the Madagascan geckonid genus *Paroedura,* which had to be split off from the paraphyletic *Phyllodactylus* (that means for zoological and not for nomenclatural reasons) (DIXON & KROLL 1974). But unfortunately, specific names such as *Phyllodactylus pictus* remained unchanged as *Paroedura pictus* for some time, certainly not because of an intended "virtue of stability" of the respective authors, but much more likely because of a lack of Greek and Latin knowledge which lead to the ignorance of Art. 34.2. of the Code; or the amendment of endings has simply been forgotten in this and other cases. Fortunately, NUSSBAUM & RAXWORTHY (2000) provided the correct spellings in their recent revision of the genus.

If a changing ending of a name is thought to threaten stability and universality, the Code (ICZN 1999) would have to be altered in that the endings of adjective, flectible specific names would not have to follow the gender of the genera any more, i.e. Article 31.2. would have to be deleted. But this would at the same time destroy the philological basis on which the whole system of biological nomenclature is built, viz. the Greek and Latin languages. Our view is furthermore supported by Article 30.1.4.2. of the current edition of the Code (ICZN 1999), which clearly states that "a genus-group name that is or ends in a word of common variable gender (masculine or feminine) is to be treated as masculine unless its author, when establishing the name, stated that it is feminine or treated it as feminine in combination with an adjectival species-group name". This article probably applies to several other cases where the genus' gender was not determined in the original description and therefore more changes of adjectival species-group names from feminine to masculine are to be expected. If such actions threaten stability, the Code would be self-contradictory – we think it is not.

A last point which we should like to address here is ARNOLD's (2000) final recommendation: "However, ... changes, for instance when a group within a known clade is separated as a new genus, can be avoided by using subgenera". This proposal considers genera simply as operational units and is contra productive to modern efforts for a new, less arbitrary generic concept (see e.g. DUBOIS 1988), which includes biological reality and takes into account that the genus, in spite of all subsequent higher categories, is the classificatory level above the species where reticulate evolution just begins to stop.

In conclusion, by considering: (1) that WAGLER (1830) did not combine the generic name *Podarcis* with any species name and therefore did not demonstrate the intended gender of the genus; (2) that the name *Podarcis* is most probably derived from the Greek adjective 'podarkes' (Latinized: 'podarcis') and hence is of variable gender (masculine or feminine); (3) that the Principle of First Reviser does not apply to determination of gender of names; and (4) that the Code (ICZN 1999) clearly states that a name of common variable gender is to be treated as masculine, we hereby reassert that the gender of *Podarcis* must be considered masculine.

Acknowledgements. We are indebted to two anonymous reviewers for useful comments and to Anthea Gentry (ICZN) for further discussion.

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Received:	13.06.2002
Accepted:	09.01.2003
Revised:	21.06.2004
Corresponding editor:	M. Schmitt

Bonner zoologische Beiträge	Band 53 (2004)	Heft 3/4	Seiten 297–301	Bonn, Dec. 2005

Morphology, Genitalia, and Natural History Notes on the Enigmatic Tiger Beetle, *Mantica horni* Kolbe, 1896 (Coleoptera, Cicindelidae)

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Abstract. The morphology of the extremely rarely collected tiger beetle, *Mantica horni,* is described on the basis of a large series from a new locality near Maltahöhe, southern Namibia. Male genitalia and female external genitalia are described for the first time and compared with those of the presumed sister genus, *Manticora*. Additionally, we firstly report on habitat and behaviour of the species.

Key words. *Manticora*, habitat, Namibia.

1. INTRODUCTION

The cicindelid tribe Manticorini consists of two genera, *Mantica* Kolbe, 1896 and *Manticora* Fabricius, 1792 and contains very large, crespuscular to nocturnal, exclusively southern African species. In contrast to the comparably well known genus *Manticora* (e.g., KLUG 1849; ROER 1984; MAREŠ 1976, 1995, 1997, 2002; LEFFLER 1980; WERNER & WIESNER 1994, 1995; WERNER 2000), the only species of the genus *Mantica*, the southern Namibian *M. horni* Kolbe, 1896, is regarded as extremely rare and its biology is virtually unknown. Since the original description, which is based on two males (KOLBE 1896), only a very few additional individuals have been collected, most of them presumably incidentally (MAREŠ 1976, 2002; WERNER & WIESNER 1994, 1995; WERNER 2000). Comprehensive information on the morphology of the species is only given in the original description, where KOLBE (1896) presents a fairly good description of the two male syntypes (for an English translation of the original description see PÉRINGUEY 1896). Subsequently, there were almost no data added, with the exception of a few comparative features mentioned by HORN (1910) and some basic habitat data ("Sand plateau on top of the Fish River Canyon without almost no vegetation", "long grass and other scattered plants near Karasburg") by MAREŠ (2002). Most recently, good photographs of almost all collected specimens including one of the syntypes (not "holotype" as mentioned by MAREŠ 2002) were published by WERNER & WIESNER (1994), WERNER (2000), and especially MAREŠ (2002). However, until today almost any detailed information on habitat, biology and even female morphology are lacking.

In February 2003, O. and W. Heinz discovered a mass aggregation of *Mantica horni*. This gave us the opportunity to report firstly on certain aspects of the morphology, genitalia, habitat, behaviour, and prey of this enigmatic species.

2. MATERIAL AND METHODS

In total 45 specimens (24 males, 21 females) were examined. The series was collected on 5 February 2003, approximately 3-5 km W of Maltahöhe (Namibia, Hardap district) at the upper course of the Hudup River (a tributary of the Fish River), 24°50'S, 16°54'E, 1300 m a.s.l. All specimens are currently in the authors' collections.

MAREŠ (1995) found no distinguishing characters among male genitalia of *Manticora* species. Consequently, we compared *Mantica* genitalia only with one male of *Manticora livingstoni* from 30 km E of Rundu, Namibia, and one female of *Manticora* cf. *latipennis* from an unknown locality in the Republic of South Africa (both in the collection of M. Franzen).

Measurements taken are: total length (without labrum), body width (across the widest points of the elytrae), and elytral length. The internal sacs of two male aedeagi were gradually blown out with water. Toothpaste was than injected into the fully blown out sacs to keep them in form; finally they were fixed and stored in 5% formaldehyde solution. Female genitalia were removed from two individuals, which had their ovipositors everted. The nomenclature of the male genitalia follows ISHIKAWA (1978) and MATALIN (1998), and those of the female genitalia FREITAG (1972).

3. RESULTS

3.1. Description

3.1.1. Morphology. Coloration entirely shiny black. **Head.** Antennal scape and antennal segments 2 to 4 with scattered semierect setae additionally to sensories (Fig. 1a). Left mandible (Fig. 1b, c) slightly longer than right in males; in a very few individuals mandible lengths appear almost equal; mandible lengths equal in all females; outer basal half of mandibles with long erect setae. Labrum (Fig. 1d) much wider than long, with 6-10 (mostly 8) submarginal setae; indistinctly quadridentate, "teeth" appear as rounded bulges. Clypeus with some 12-15 long erect setae. Frons and vertex smooth (except for setigerous punctures), shiny; frons with median field of long erect setae, extending anteriorly to eyes; a conspicuous ridge present from above insertation of antennae to middle of eye; row of four supraorbital setae extending posteriorly to irregular row of 10-12 setae submarginally across head. Eyes small. Genae with scattered, long, erect, thin setae. **Prothorax.** Pronotal shape globose, with very deeply impressed anterior and posterior transverse sulci, latter forming two somewhat rounded-triangular, posteriorly reaching lobes; a minute bulge at posterior angle; median longitudinal sulcus indistinct if visible; a short lateral bead extends from shortly after anterior transverse sulcus to posterior third of pronotum; pronotal surface shiny, with scattered long, erect setae along anterior, posterior, and lateral margins; anterior setose margin reaching to anterior transverse sulcus, lateral margin reaching onto disc; centre of disc almost glabrous except some single short setae. Proepisterna shiny with smooth surface. Prosternum with transverse ridge bearing row of short erect setae. **Pterothorax.** Mesepisterna glabrous, females lack coupling sulcus. **Elytra.** Shape of elytrae ovoid, apically pointed, shoulders rounded; surface of elytrae and epipleura of elytrae with numerose large carinate tubercles (largest ending in a cylindrical cone), each one bearing a fine, long seta at its posterior base; tubercles have their highest point posteriorly; tubercles very small and almost lacking on anterior elytrae along suture and densest and highest within apical third of elytrae; apically largest tubercles form two oblique, serrated ridges, starting at posterior central third and extending to apical tip of suture. **Abdomen.** Sterna with transverse rows of fine, long semierect setae. **Legs.** Coxae with fine long setae, densest posteriorly; trochanters adpressed setose; femora, tibiae, and tarsomeres with dense cover of thick, black, erect setae; tarsi not dilated in males.

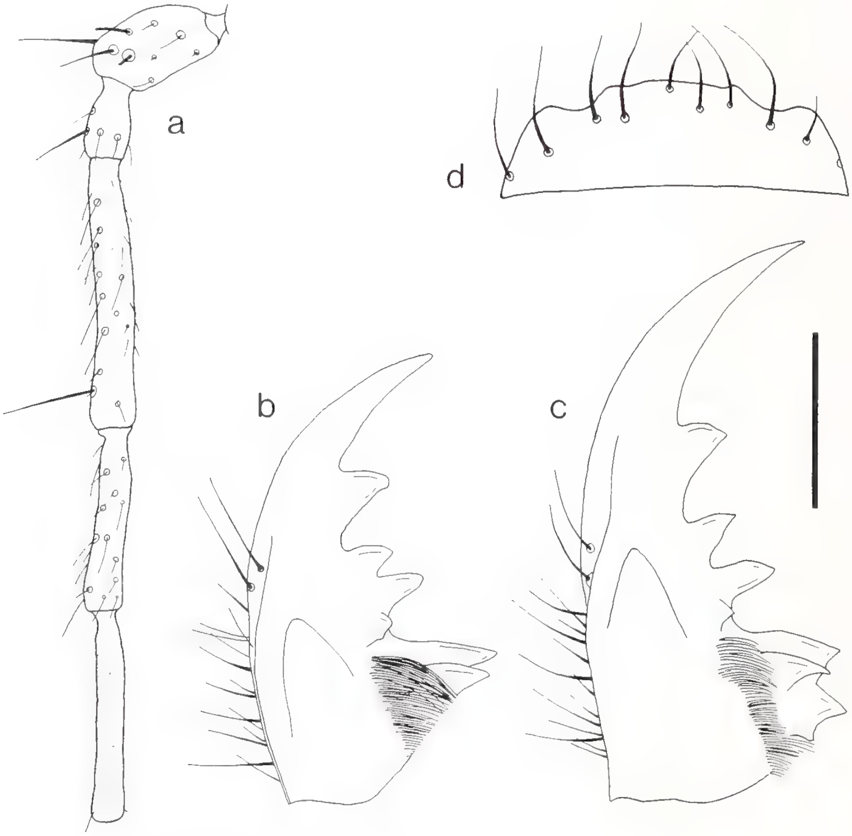

Fig. 1: *Mantica horni.* **a)** first five antennal segments, male; **b)** left mandible, female; **c)** left mandible, male; **d)** labrum, male. Scale bar: 2 mm.

3.1.2. Male genitalia. Shape of aedeagus moderately elongate and evenly curved, with considerably thickened basal part and very tiny apical knob (Fig. 2c); it lacks any structures like concavities, lateral flanges or lobes; dorsal ostium (apical orifice) very long, forming about 40% of aedeagal length, and basally divided by narrow, sclerotized thorn (Fig. 2c). Internal sac (Fig. 2a, b) strongly elongate, with large and protuding, thumb-like basal bladder; dorsally a long sclerite which is probably identical with ligula sensu ISHIKAWA (1978). Truncal tube extremely elongate, formed by basi-lateral right bladder. Sclerites and bladders on apical portions only indistinctly discernible in our specimen. The identifiable stuctures include a prominent praeputial pad, very long flagellum, relatively small medial tooth, upper limitator, and shield (Fig. 2a, b).

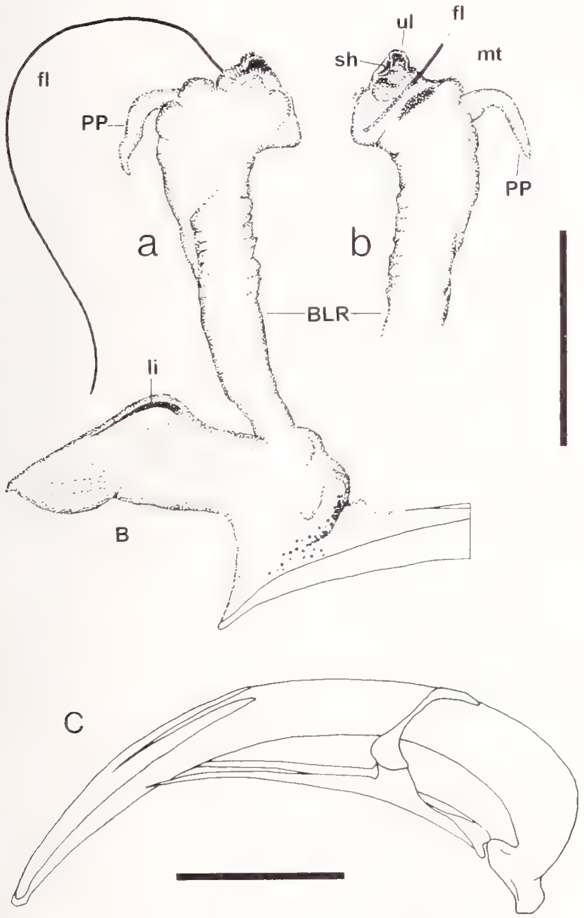

Fig. 2: Male genitalia of *Mantica horni*. **a)** internal sac, right lateral view; **b)** apex of internal sac, left lateral view; **c)** adeagus. Sclerites: fl = flagellum, li = ligula, mt = median tooth, sh = shield, ul = upper limitator; bladders: B = basal bladder, BLR = basi-lateral right bladder, PP = praeputial pad. Scale bars: 3 mm.

The aedeagus and the general internal sac proportions and structures resemble those of *Manticora livingstoni* almost completely. The only exception is the lack of a praeputial pad in *Manticora*. However, it may be that this structure has been incompletely blown in the latter.

3.1.3. Female external genitalia. In two females ovipositors everted with a length of 32-34 mm (oviduct + ovipositor). Sternum eight (Fig. 3a, b) apically broadly rounded, with narrow, triangular medial emargination; apex with numerous short, fine setae. Second gonocoxa with no ventral groove or notch, inner apical sides with some scattered very fine short setae (Fig. 3a). Second gonapophyses short and broad; lateral portions somewhat triangular and distinctly shorter than medial, both portions curved dorso-medially (Fig. 3a, b). Syntergum 9&10 appearing somewhat ovoid with lateral portions slightly pointed at apex (Fig. 3c); apical two-thirds of lateral portions with numerous setae.

Female external genitalia of *Manticora* resemble those of *Mantica horni* almost completely, with the exception of less broadened medial and lateral portions of second gonapophyses, less pointed lateral portions of syntergum 9&10, and the overall larger size in *Manticora*.

3.1.4. Sexual dimorphism. Besides different mandible lengths and a tendency to have the left mandible longer than the right in males (see above), there are several morphometric characters which separate males from females: males have slightly shorter total lengths than females and possess shorter and narrower elytra (see Table 1.: EL/TL, BW/TL, BW/EL).

Table 1: Morphometric values of *Mantica horni*. TL = total length; EL = elytral length; BW = body width.

	TL	EL/TL	BW/TL	BW/EL
Males (n = 24)				
mean	28.0	0.60	0.39	0.66
standard deviation	1.08	0.01	0.01	0.03
range	26.0-30.0	0.58-0.62	0.37-0.41	0.61-0.71
Females (n = 21)				
mean	30.0	0.62	0.42	0.69
standard deviation	1.11	0.01	0.01	0.02
range	27.5-32.0	0.59-0.65	0.40-0.44	0.66-0.73

3.2. Habitat and natural history observations

All specimens were collected from a gravel road leading between the Hudup River and the south-facing slopes of the directly adjoining hilly terrain. The steep slopes (inclination about 30°) were rocky and had about 40% rocks, stones and gravel on the surface, with interspersed fine loamy substrate. However, loamy areas dominated near to the river. The vegetation consisted of grasses and shrubs, with interspersed thorn bushes. Vegetation cover was approximately 50%, with bushes making about 15%.

On February 5, the locality was visited two times. During the first visit, about two hours before dusk, no beetles were observed. Returning one hour later, the mass aggregation was observed. From that time activity continued until dusk and then markedly decreased. During the observations the weather was clear and air temperature was around 30°C. On the previous day, a heavy thunderstorm brought the first heavy rains after a long dry season and there was much humidity around with puddles and small rivulets along the road. The locality was revisited in early morning of the next day, but without finding any more *Mantica*.

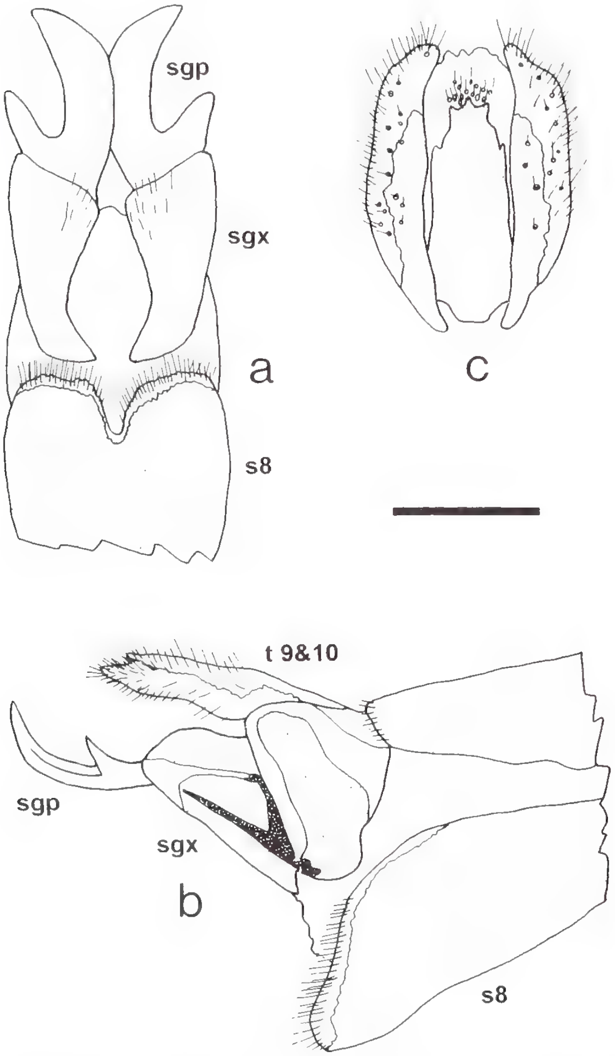

Fig. 3: Female external genitalia of *Mantica horni*. **a)** apex of sternum, ventral view; **b)** apex of sternum, lateral view; **c)** syntergum 9&10, dorsal view. s8 = sternum eight, sgp = second gonapophysis, sgx = second gonocoxa, t9&10 = syntergum 9 & 10. Scale bar: 2 mm.

It appeared that during the beginning of the observations beetles' movements were directed downhill towards the road/river. Later, individuals stayed on the road. Coupling pairs comprised about 30% of the beetles observed. In addition, two females were presumably taken during oviposition because they had their ovipositors everted. Most individuals (including mating couples) were found actively foraging on swarming termites. Movements were fast and if disturbed, individuals tried to escape by running even more quickly into dark, shaded areas (e.g., under the car). Single individuals or couples were observed every 10 to 100 m along the road.

Although no individuals of the series were teneral, three males possessed comparably soft aedeagi and it appears that hardening after emergence may not have been fully completed in these individuals. Thus, at least a part of the series may have been taken only several days after emergence (see WILLIS 1967: 189-190 for a timetable of hardening after emergence in some North American *Cicindela*).

4. DISCUSSION

The new locality extends the known range of the species some 190 km to the north (measured from the formerly known northernmost precise locality ("Bethanien [Hanam Plateau]": WERNER & WIESNER 1994). Despite this considerable range extension, we could not find any obvious morphological differences among our new material and the previously collected specimens (compared with the photographs in MAREŠ 2002; WERNER 2000; WERNER & WIESNER 1994). We found only one external character mentioned by KOLBE (1896), which is differing in our new material: KOLBE (1896) states that right and left mandible lengths are equal in males. Although indistinctly visible in some individuals, most of our males possess a slightly longer left mandible.

The close relationship of *Mantica* and *Manticora* is stressed by several unique characters (see also MAREŠ 2002): both genera possess unequal mandible lengths in males (but character heterogenous in *Mantica*), lack dilated tarsi in males, possess ciliated apical palpal segments and long setae on the outer mandible sides, have similar organized dorsal elytral tubercles which form two oblique ridges apically, and have rather similar male and female genitalia. By contrast, both genera are well separated by the longer, asymmetrically formed mandibles of *Manticora,* more labral teeth in *Manticora* (6 vs. 4), the generally much more "robust" habitus of all *Manticora* species, which is basically expressed by broader heads and elytrae, and pronounced bulged elytral shoulders.

The observations at Maltahöhe indicate that short surface activity of *Mantica* is linked with rare and strongly localized rains in its arid habitats. WERNER (2000) mentioned several observations that *Manticora* species were found abundantly under the same conditions, i.e. hunting for myriapods and tenebrionids after rainfall. Prey items have never been reported for *Mantica*, but we presume that the species is an opportunistic feeder, predominantly preying on such invertebrates, which share their seasonal surface activity with the tiger beetle.

Acknowledgements. Many thanks to Jürgen Wiesner (Wolfsburg), who provided – once again – important literature and commented a previous draft of the manuscript. We are also grateful to two anonymous reviewers for their helpful comments.

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Received:	09.12.2003
Revised:	09.06.2005
Accepted:	10.06.2005
Corresponding editor:	M. Schmitt

Bonner zoologische Beiträge	Band 53 (2004)	Heft 3/4	Seiten 303–310	Bonn, Dec. 2005

On the Taxonomy and Biogeography of *Stenus* (s. str.) *erythrocnemus* Eppelsheim and Related Species (Insecta: Coleoptera: Staphylinidae)

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Abstract. Material previously identified as *Stenus erythrocnemus* Eppelsheim, *S. anatolicus* Puthz, and *S. maculiger* Weise is revised with special reference to the internal structures of the aedeagus. Three new species of *Stenus* s. str. are described, illustrated, and distinguished from similar congeners: *S. cypriacus* **sp. n.** (Cyprus), *S. distortus* **sp. n.** (Anatolia), and *S. prominens* **sp. n.** (Lebanon, Israel). The distributions of *S. cypriacus, S. distortus, S. erythrocnemus, S. anatolicus*, and *S. maculiger* are mapped. The morphological variation of the male sexual characters of *S. erythrocnemus* and *S. maculiger* is illustrated and discussed.

Key words. Palaearctic – Europe – Turkey – Cyprus – Lebanon – new species – distribution

1. INTRODUCTION

Among the Palaearctic species of the subgenus *Stenus* Latreille with spotted elytra, a species group can be identified which is characterized by a conspicuous – evidently synapomorphic – sclerotized basal structure in the internal sac of the aedeagus. In the Western Palaearctic, this group comprises *Stenus erythrocnemus* Eppelsheim, *S. maculiger* Weise, *S. anatolicus* Puthz, and *S. sacrimontis* Puthz. The sclerotized internal structures of *S. anatolicus*, *S. erythrocnemus*, and *S. sacrimontis* were figured by PUTHZ (1970a, b), but their intra- and interspecific variation has never been studied.

When comparing recently collected material of *S. anatolicus* from southern Anatolia with males previously identified as *S. anatolicus* and recorded as such from Cyprus (ASSING & WUNDERLE 2001), I became aware of some evident differences, not only in the size and shape of the median lobe, but especially in the morphology of the basal internal structure of the aedeagus. A subsequent more systematic study of the internal structures of males previously identified as *S. erythrocnemus* and *S. anatolicus* from several public and private collections then revealed the existence of three undescribed species, one from Cyprus, one from Anatolia, and one from Lebanon and Israel.

2. MATERIAL AND MEASUREMENTS

The material treated in this study is deposited in the following public and private collections:

FMNH	Field Museum of Natural History, Chicago (A. Newton)
MHNG	Muséum d´Histoire Naturelle, Genève (G. Cuccodoro)
NHMW	Naturhistorisches Museum Wien (H. Schillhammer)
UH	University of Haifa
cAss	author´s private collection
cFel	private collection B. Feldmann, Münster
cPut	private collection V. Puthz, Schlitz
cRos	private collection A. Rose, Oldenburg
cSch	private collection M. Schülke, Berlin
cWun	private collection P. Wunderle, Mönchengladbach

The measurements are given in mm and abbreviated as follows: HW: head width across (and including) eyes; PW: maximal width of pronotum; PL: length of pronotum along median line; EL: length of elytra from apex of scutellum to elytral hind margin; EW: width of elytra; ML: length of median lobe of aedeagus.

3. *STENUS* (S. STR.) *ERYTHROCNEMUS* EPPELSHEIM AND RELATED SPECIES

3.1. *Stenus anatolicus* Puthz (Fig. 1, Map 1)

Types examined: Paratype ♂: Anatolia mer., Korge & Heinz leg. / Pisid. Taurus, Bozburun, 1600-2000m, 20.VII.65 / ♂ Paratype / Stenus anatolicus n. sp. det. V. Puthz 1968 (cPut). Two examined paratypes from Maraş are not conspecific with the paratype from Bozburun, which was collected together with the holotype, and are now listed as paratypes of *S. distortus* sp. n. (see below).

Additional material examined:

Turkey: Muğla: 1♂, Dalaman, 27.V.1991, leg. Schönmann & Schillhammer (cPut). **Antalya:** 1♂, Fakircali, 22 km NE Demirtas, 600-700m, 4.V.1997, leg. Schulz, Vock & Sanetra (cAss); 1♂, 1♀, E Kumluca, 36°21´50N, 30°22´27E, 385m, stream bank, 3.IV.2002, leg. Assing & Wunderle (cAss); 1♀, SSW Antalya, Çiralı, 36°25N, 30°28E, 20-50m, stream bank, 4.IV.2002, leg. Assing & Wunderle (cAss); 1♂, Kemer, 3.-15.VII.1989, leg. Schmid (cPut); 1♂, 1♀, Bey Dağları, V.1968, leg. Fagel (cPut); 1♀, 3 km W Çiralı, 36°25´27N, 30°26´41E, 71m, stream bank, 28.III.2001, leg. Rose (cRos).

Isparta: 1♂, S Eğridir, Dedegöl Dağ, N-slope, 1300-1800m, 28.-29.VII.1971, leg. Heinz (cPut).

Mersin: 7♂♂, 2♀♀, Hacıiskakli, 27.IV.1978, leg. Besuchet & Löbl (MHNG, cPut, cAss).

Mersin or Karaman: 1♂, S Karaman, Sertavul pass, ca. 1600m, 13.V.1970, leg. Zwick (cPut).

Locality ambiguous: 1♂: "Yeniköy, Toros", 30.VIII.1947 (cPut); 1♀, same data, but 29.-31.VII.1947 (cPut).

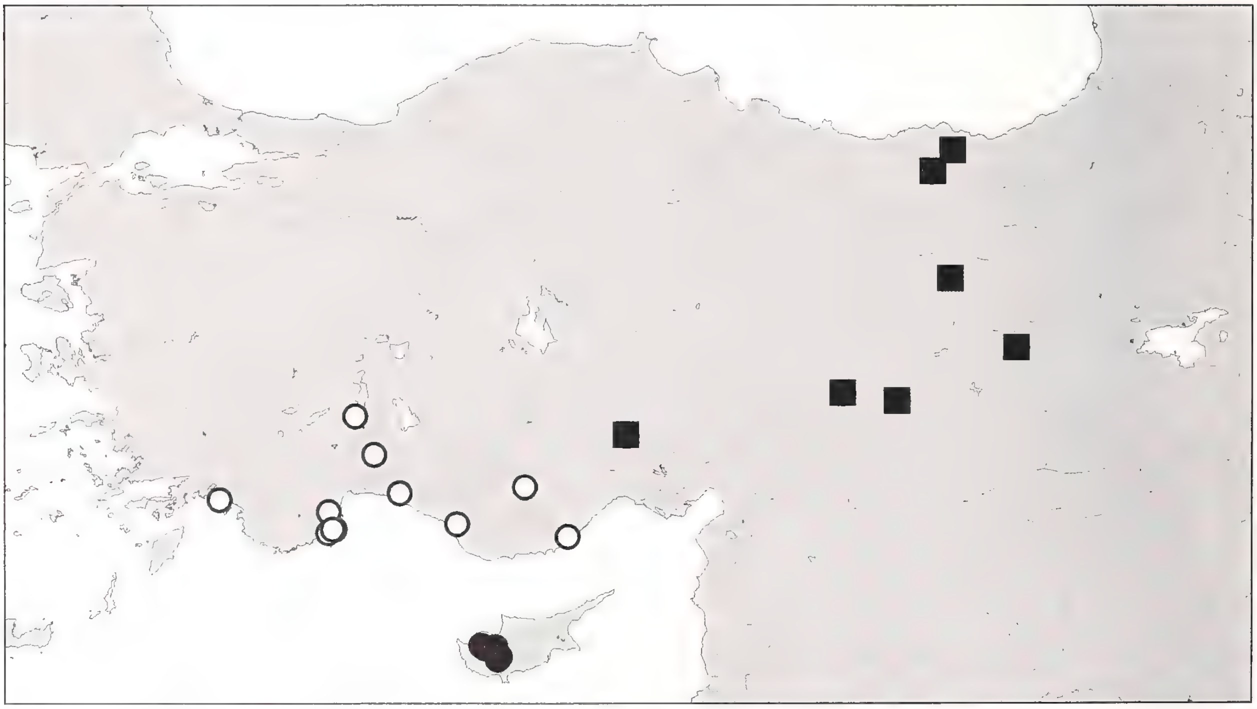
Measurements (mm) and ratios (range; n=7): HW: 0.91-0.98; PW: 0.68-0.72; PL: 0.76-0.83; EL: 0.92-1.03; EW: 1.01-1.10; ML: 0.86-0.92; HW/PW: 1.30-1.35; PL/PW: 1.08-1.15; EL/PL: 1.22-1.29; EL/EW: 0.90-0.94.

Comments: This species has been confounded with various other congeners, especially with the following three undescribed species and with *S. erythrocnemus*. Even the paratypes from Maraş are not conspecific with the holotype (see types of *S. distortus* sp. n.). Among the closely related species, *S. anatolicus* is identified by the shape of the aedeagus and by the untwisted basal internal structure of the median lobe (Fig. 1). For additional, but less reliable characters see the remarks below the following species. A detailed description of the external characters is given by PUTHZ (1970a).

Distribution: The distribution of *Stenus anatolicus* is apparently confined to southwestern Turkey from Muğla in the west to central Mersin in the east (Map 1), a distribution pattern not uncommon among Turkish Staphylinidae. Records from other regions refer to one of the following species.

3.2. *Stenus* (s. str.) *cypriacus* sp. n. (Figs. 2, 7, Map 1)

Types: Holotype ♂: CYPRUS – S Platres, Moniatis, Bachtal, Bachufer, 700m, 12.IV.1995, Assing / Holotypus ♂ *Stenus cypriacus* sp. n. det. V. Assing 2002 (cAss). Paratypes: 5♀♀: same data as holotype (cAss); 1♂: same data as holotype, but 07.IV.1995 (cAss); 2♂♂, 3♀♀: Cyprus, Commanderia, B8 b. Moniatis, 750m, Bachschlucht, 2.-12.4.95, P. Wunderle (cWun); 1♂, 1♀: Chypre, 700m, Kalopanayiotis, 17.VII.1977, C. Besuchet (MHNG); 1♂: CIPRO Val. Cedri, m. 1300m, 25.4.63, Henrot-Cerruti (cPut); 1♂: Cypr. Stavros, 18.-



Map 1: Distributions of *Stenus anatolicus* Puthz (open circles), *S. cypriacus* sp. n. (filled circles), and *S. distortus* sp. n. (black squares) in Turkey and Cyprus, based on examined material.

19.7.39, Håkan Lindb. / Field Mus. Nat. Hist. 1972, Ludwig Benick Colln. Acc. Z-14, 869 (FMNH); 1♀: ZYPERN, Mesopotamos, 32°54′/34°53′, 5.5.74, MALICKY (cPut); 1♂: Troodos, 11.6.1963, leg. T-E. Leiler (cWun).

Description: Measurements (mm) and ratios (range; n=7): HW: 0.86 - 0.94; PW: 0.65 - 0.69; PL: 0.71 - 0.76; EL: 0.91 - 0.98; EW: 0.98 - 1.06; ML: 0.72 - 0.76; HW/PW: 1.33 - 1.39; PL/PW: 1.09 - 1.16; EL/PL: 1.22 - 1.30; EL/EW: 0.91 - 0.94.

External characters as in *Stenus anatolicus* (Fig. 7), but of smaller average size (see measurements) and antero-lateral tubercles on pronotum mostly obsolete. (In *S. anatolicus* the tubercles are usually distinct.) Bases of femora (as in *S. anatolicus*) usually distinctly lighter (yellowish to reddish brown) than apical halves.

♂: secondary sexual characters similar to those in *S. anatolicus*: sternite VI slightly flattened and with weakly concave posterior margin; sternite VII with relatively long and dense testaceous pubescence, shallowly, but extensively impressed in posterior half, posterior margin broadly and distinctly concave; sternite VIII weakly impressed before the broadly concave posterior margin; sternite IX similar to that of *S. anatolicus*; aedeagus of similar general morphology as in *S. anatolicus*, but distinctly smaller (see measurements and Fig. 2), apically more abruptly narrowed, and basal internal structures of completely different shape (Fig. 2).

Etymology: The name is an adjective and refers to the fact that the species is apparently endemic to Cyprus.

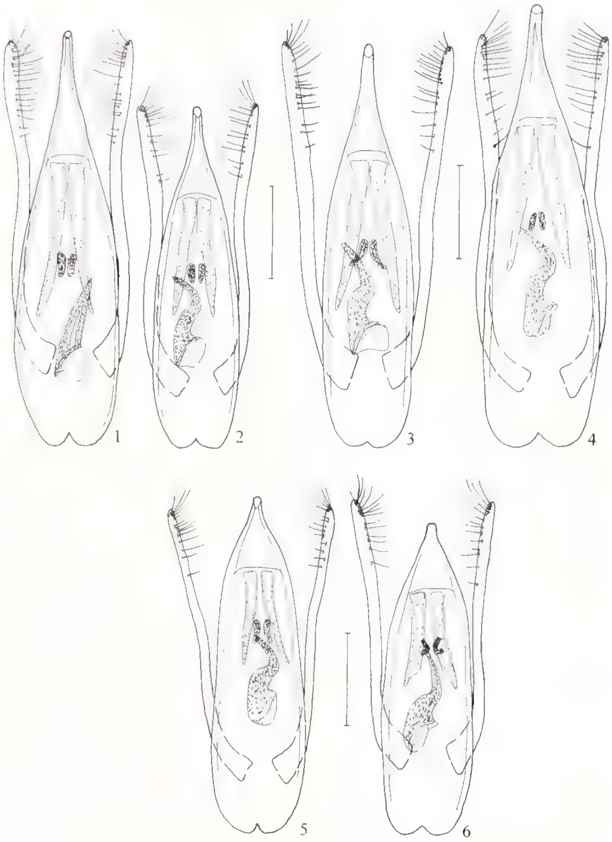
Comparative notes: In the related species with a similarly shaped aedeagus (*S. anatolicus*, *S. distortus*, *S. prominens*), the median lobe of the aedeagus is distinctly larger (see measurements and figures), the basal internal structure of the internal sac is of completely different shape (*S. anatolicus*) or smaller and more slender (*S. prominens*, *S. distortus*), the antero-lateral tubercles on the pronotum are usually more distinct (*S. anatolicus*, *S. distortus*), the size is on average larger (see measurements), and the femoral bases are not distinctly lighter than the apices (*S. distortus*).

Distribution: *Stenus cypriacus* is presumably endemic to Cyprus (Map 1). It is known from several localities, but according to personal observations it is not abundant. The records of *S. guttula* Müller in BAUDI DI SELVE (1870) and of *S. anatolicus* in ASSING & WUNDERLE (2001) refer to this species.

3.3. *Stenus* (s. str.) *distortus* sp. n. (Fig. 3, Map 1)

Stenus anatolicus Puthz, 1970a (PUTHZ 1970a: 22ff) partim.

Types: Holotype ♂: TR – bor., Torul, 9.6.1994, leg. Scoupý / Holotypus ♂ *Stenus distortus* sp. n. det. V. Assing 2002 (cAss). Paratypes: 1♂, 4♀♀: same data as holotype (cFel, cAss); 1♂: Turkey, 2.8.86, Maçka -> Sumela, leg. Feldmann (cFel); 1♂, Quelle am Tunnel vor Sürgu, Taurus / 13.V.1970, Zwick leg. / SO-Anatolien, Ost-Taurus bei Sürgü, 13.V.1970, Zwick (cPut); 2♂♂, 3♀♀: Anatolia mer., Heinz leg. / Höhle an z.T. subterranem Fluß, ca. 61 km südl. v. Bingöl, 9.VII.1974 (cPut, cAss); 1♂: Türkei, Taurus, Bolkar Daglari, Umg. Ciftehan (Flußufer, ca. 1500 mNN), 26.VI.1990, leg. Zeuner (cPut); 1♂: ca. 80km NW Maraş, Türkei, Zwick leg. / 16.V.1970, Bach a. d. Schneegr. / ANATOLIEN, 10.-22.5.1970, leg. Zwick (cPut); 1♂, Türkei, 17.5.1969, Maraş, leg. Wewalka (cPut); 1♂, 3♀♀: TURKEY: 14.-19.vii.2000, Adiyaman prov.; Nemrut Daği Mts., Karadut env., I. Smatana leg. (cSch, cAss); 1♂, 1♀: Maraş, 17.5.69, leg. Wewalka / Paratype / Stenus anatolicus n. sp. det. V. Puthz 1970 (MHNG).



Figs. 1-6: Aedeagus of *Stenus anatolicus* Puthz (1), *S. cypriacus* sp. n. (2), *S. distortus* sp. n. (3), *S. prominens* sp. n. (4), *S. erythrocnemus* Eppelsheim (5), and *S. maculiger* Weise (6). Scale: 0.2 mm.

Description: Measurements (mm) and ratios (range; n=7): HW: 0.91 - 1.00; PW: 0.71 - 0.79; PL: 0.77 - 0.89; EL: 0.95 - 1.09; EW: 1.06 - 1.16; ML: 0.83 - 0.94;

HW/PW: 1.25 - 1.35; PL/PW: 1.06 - 1.17; EL/PL: 1.19 - 1.29; EL/EW: 0.88 - 0.94.

Externally highly similar to *S. anatolicus*, but femoral bases usually not or only indistinctly lighter than apical halves and pronotum on average wider (see measurements). ♂: aedeagus of similar shape and size, but basal internal structure twisted, of completely different shape (Fig. 3).

Etymology: The name (Lat., adj.: twisted) refers to the shape of the basal internal structure of the aedeagus, which readily separates this species from *S. anatolicus*, with which it was previously confused.

Comparative notes: For separation from *S. anatolicus* see description. *S. cypriacus* has a smaller aedeagus with a smaller and more slender basal internal structure; in addition, the body is on average smaller (little overlap, see measurements). In *S. prominens*, the apex of the median lobe of the aedeagus clearly extends beyond the parameres. In both *S. cypriacus* and *S. prominens* the femora are basally lighter and the antero-lateral tubercles on the pronotum are indistinct or obsolete.

Distribution: *Stenus distortus* is known from northern, central southern, and eastern Anatolia (Gümüşhane, Trabzon, Malatya, Bingöl or Diyarbakir, Niğde); its known distribution does not overlap with that of *S. anatolicus* and *S. erythrocnemus* (Map 1).

3.4. *Stenus* (s. str.) *prominens* sp. n. (Fig. 4)

Types: Holotype ♂: LIBANON, Touaite / Holotypus ♂ *Stenus prominens* sp. n. det. V. Assing 2002 (cPut). Paratypes: 1♀: Libanon, VI.1995, Ehden, 1500m, Horch Ehden, Bach, leg. C. Reuter (cFel); 1♂: ISRAEL, Banias, 1.VII.1986, A. Shlagman / G. Haghebaert coll. & det., Stenus s. str. guttula Müll. (UH).

External morphology as in *S. anatolicus*, but with indistinct or obsolete antero-lateral pronotal tubercles and with basal halves of femora testaceous to rufous. ♂: median lobe of aedeagus large, apically distintly extending beyond parameral apices; basal internal structure twisted (Fig. 4).

Description: Measurements (mm) and ratios (holotype, ♂ paratype): HW: 1.04, 1.01; PW: 0.77, 0.76; PL: 0.85, 0.85; EL: 0.98, 1.00; EW: 1.07, 1.00; ML: 0.94, 0.94; HW/PW: 1.35, 1.34; PL/PW: 1.10, 1.12; EL/PL: 1.16, 1.18; EL/EW: 0.92, 0.92.

Etymology: The name (Lat., adj.: protruding, exceeding, standing out) refers to the long apex of the median lobe of the aedeagus, a character distinguishing this species from its closely related congeners.

Comparative notes and discussion: From the other Eastern Mediterranean representatives of the *S. erythrocnemus* goup, *S. prominens* is distinguished especially by the apically long median lobe of the aedeagus, and by the shape of the basal internal structure. In addition, it is separated from *S. anatolicus*, *S. distortus*, and *S. erythrocnemus* by the indistinct or obsolete antero-lateral pronotal tubercles, from *S. distortus* and *S. erythrocnemus* by much lighter femoral bases, and from *S. cypriacus* by larger size.

Distribution: *Stenus prominens* is known from three localities in Lebanon and Israel.

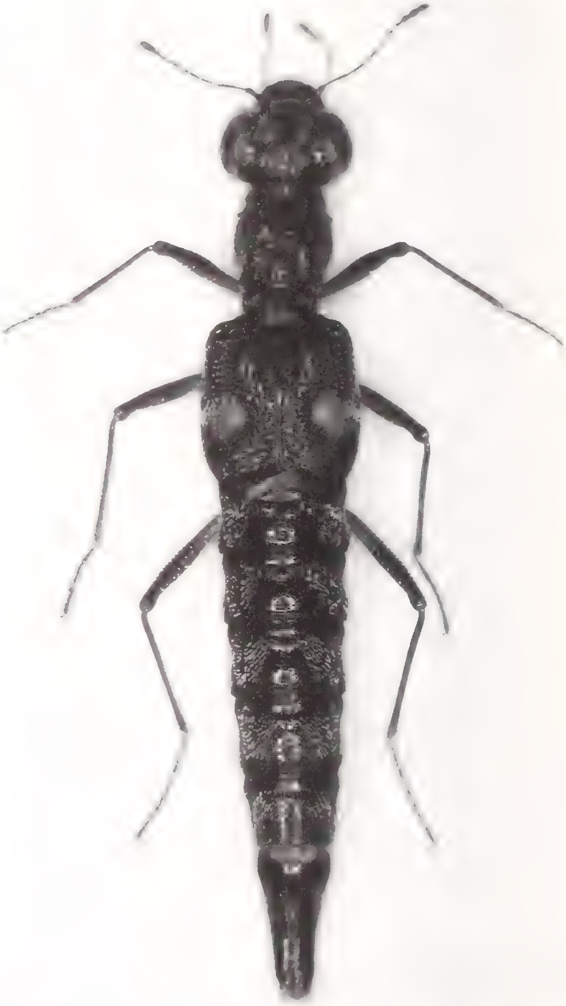


Fig. 7: *Stenus cypriacus* sp. n.

3.5. *Stenus erythrocnemus* Eppelsheim (Fig. 5, Map 2)

Type examined: Syntype ♀: Lenkoran, Leder (Reitter) / 15. / 10. / c. Epplsh. Steind. d. / erythrocnemus Epp. Typ. / TYPUS (NHMW).

Additional material examined:

Turkey: Artvin: 5♂♂, 7♀♀, Artvin-Savsat, 4.VI.1989, leg. Schönmann & Schillhammer (NHMW, cPut, cAss); 1♂, Borçka, 27.VI.1970, leg. Schubert (NHMW); 3♂♂, 1♀, Borçka, 1700m, 18.-27.VI.1970, leg. Schubert (NHMW, cPut); 6♂♂, Borçka, VII.1971, leg. Schubert (NHMW); 5♂♂, 4♀♀, Borçka, VII.1974, leg. Schubert (NHMW, cPut, cAss); 1♂, pass between Murgul and Arhavi, 1000-1200m, 17.VII.1972, leg. Heinz (cPut). **Rize:** 1♀, Ardeşen, Ilica, 20.V.1970, leg. Zwick (cPut); 3♂♂, 3♀♀, Firtina valley, 1300m, leg. Vit (MHNG, cPut, cAss). **Locality not identified:** 1♂, Karçkal – Otingo, 1200-1600m, 10.-12.VII.1983, leg. Heinz (cPut).

Georgia: 1♂, Tbilisi, leg. Leder (Reitter) (cPut); 2♂♂, 6♀♀, Zchneti near Tbilisi, 20.VII.1985, leg. Wrase (cPut, cSch). **Abkhazia:** 1♂, Avadkhara, 2000-2800m, 8.-13.VII.1982, leg. Wrase & Schüler (cSch).

Armenia: 1♂, 1♀, Gegemskij Chr., Geghard, 2000m, 3.VII.1989, leg. Pütz (cPut).

Iran: 9♂♂, 10♀♀, Ilam, Tchaharmelleh, 33°57N, 46°17E, 28.VI.1974, leg. Senglet (MHNG, cPut, cAss); 1♂, Teheran, above Shemshale, 2400-2800m, 18.VIII.1967, leg. Heinz (cPut); 1♂, 1♀, Kerman prov., 1964, leg. Löffler (cPut); 1♂, Kermānshāh, Kenesht/Kermānshāh, 34°29N, 47°09E, 3.VIII.1973, leg. Senglet (cPut); 2♂♂, Fars, ca. 50 km W Shiraz, Dasht-e-Arzhan, 1900m, 21.IX.1997, leg. Schödl (NHMW); 1♂, 1♀, Fars, 30 km N Nurabad, 25.IV.1996, leg. Wewalka (NHMW); 1♂, Fars, Dasht-e-Arjan, 55km NSSK W Shiraz, 22.IV.1993, leg. Pour (cPut); 1♂, 1♀, Ilam, Sarāb Eyvān, 33°45N, 46°22E, 26.VI.1974, leg. Senglet (cPut); 4♂♂, 4♀♀, Buyer Ahmad o Kuhgiluye, 30km S Yasug, spring, 25.IV.1996, leg Wewalka (NHMW, cPut, cAss); 1♂, Qars-i-Shirin, "Fiume ad W terr. nudo limo", 7.IV.1956, leg. Soika (NHMW); 1♂, SW-Iran, Hoseiniyeh, 28km NNW Andimeshk, 360m, 12.-13.IV.1977 (cAss); 1♀, Gilan, Lunak, SW Lāngrad, 700m, 2.VII.1998, leg. Heinz (cPut); 1♂, 1♀, SE-Iran, Transhar [?] (NHMW, cPut).

Pakistan: 2♂♂, Chitral, Bumburet, 2200-2350m, 24.V.1983, leg. Besuchet & Löbl (cPut).

Afghanistan: 1♂, Nurestan, SW Peč-Dara, 1200m, 9.VII.1971, leg. Kabakov (cPut).

Measurements (mm) and ratios (range, arithmetic mean; n=16): HW: 0.89 - 0.98, 0.93; PW: 0.66 - 0.74, 0.71; PL: 0.74 - 0.86, 0.79; ML: 0.66 - 0.77, 0.72; HW/PW: 1.25 - 1.38, 1.32; PL/PW: 1.04 - 1.20, 1.12

Comments: *Stenus erythrocnemus* is readily distinguished from all the preceding species by the differently shaped median lobe of the aedeagus, which is apically much more abruptly narrowed (Fig. 5). In addition, the elytra are often shorter and narrower, the hind wings sometimes of reduced length (less than twice the length of elytra), and the femoral bases are mostly dark (in this respect similar to *S. distortus*). The Iranian material differs from the specimens seen from northeastern Anatolia and the Caucasus region by the longer apex of the median lobe and the somewhat more slender and more abruptly bent apex of the basal internal structure of the aedeagus. Slight differences were also observed in the material from Pakistan. However, until the distributions of these morphs are clarified, these differences are here tentatively interpreted as an expression of clinal intraspecific variation.

Distribution: The species is distributed from northeastern Anatolia (where its range borders on that of *S. distortus*) and the Caucasus region to Iran, Afghanistan, and Pakistan (Map 2).

3.6. *Stenus maculiger* Weise (Figs. 6, 8, Map 3)

Material examined:

Austria: 1 ex., Niederösterreich, Oberndorf, Pfoisau, 3.VI.1972, leg. Rausch (cPut); 1♂, Kärnten, Zell, Hudajamagraben, 25.VI.-4.VII.1987, leg. Wunderle (cWun); 1♂, Kärnten, Eisenkappel, 1.VIII.1942, leg. Scheerpeltz (MHNG); 1♀, Eisenkappel, 600m, 9.VII.1941, leg. Scheerpeltz (MHNG).

Italy: 5♂♂, Carnia, Rio Tagliezzo, 8.&29.XI.1953, 4.VII.1954, 19.III.1957, leg. Springer (cPut); 1♀, Carnia, Rio Squalon, 15.VIII.1954, leg. Springer (cPut).

Slovakia: 1♀, Nová Sedlica, 15.VII.1961, leg. Smetana (cPut).

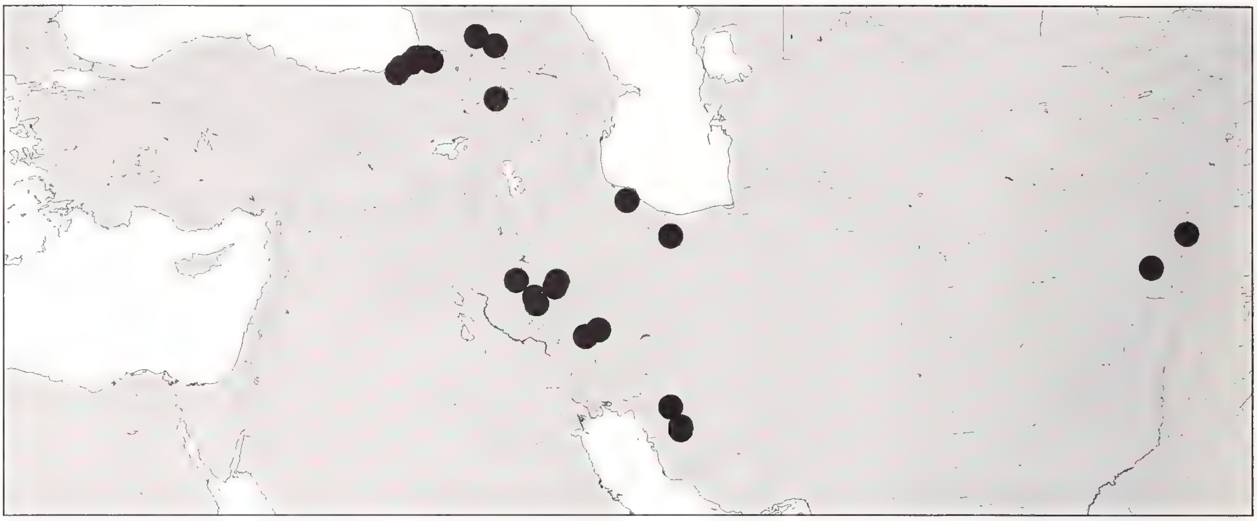
Hungary: 1♂, Mecsek range, leg. Gebhardt (cPut).

Croatia: 3♂♂, Dubrovnik, Ombla spring, 8.VIII.1958, leg. Endrödy-Younga (cPut); 8♂♂, 1♀, 1 ex., SE Dubrovnik, Mlini, 27.IX.-4.X.1968, leg. Benick (MHNG, cPut); 1♀, Dubrovnik (cPut).

Bosnia-Herzovina: 3♂♂, Jablanica (cPut); 1♂, Foča, leg. Apfelbeck (Put); 1♀, Kladanj, 1909, leg. Leonhard (MHNG); 1♀, "Herzegowina", leg. Reitter (MHNG).

Yugoslavia: Montenegro: 1♀, Mrtvica near Manastir Morača (cPut); 7♀♀, Manastir env., Morača (cPut); 2♂♂, Miločet, 4.V.1965, leg. Leiler (cPut); 1♀, 10km E Trešnjevik pass, near Andrijevica, 25.V.1979, leg. Zwick (cPut).

Bulgaria: 1♀, Nesebâr, Vlas, 17.-26.VII.1983, leg. Wrase & Schülke (cSch); 1♀, Eminska planina, Vlas, 12.V.1987, leg. Behne & Heinig (cSch); 1♀, SW-Bulgaria, Sandanski, 27.-28.IV.1985, leg. Wrase (cSch); 2♂♂, SW-Bulgaria, Samokov, 4.V.1966, leg. Löbl (cPut); 1♂, Rila, Bodrovec, 31.VIII.1966, leg. Löbl (cPut); 1♂, SW-Bulgaria, Gospodinci, 3.V.1966, leg. Löbl (cPut); 2♂♂, 1♀, Pirin, leg. Weirather (MHNG); 1♂, Sliven, X.1952, leg. Roubal (MHNG); 1♀, Sliven, 27.VI.1908, leg. Rambousek (MHNG); 1♂, Rhodopi, Pamporovo, 1500m, 28.V.1964, leg. Schulze (cPut); 1♀, Rhodopi, 5km N Schitoka lake, 41°42N, 24°36E, 22.VI.1980, leg. Malicky (cPut); 1♀, Katundere, 42°04N, 27°27E, 15.VI.1980, leg. Malicky (cPut).



Map 2: Distribution of *Stenus erythrocnemus* Eppelsheim, based on examined material. The easternmost records are in Pakistan and Afghanistan.

Albania: 2♂♂, Lumi i Bençes, Tepelene, V.1931, leg. Winkler (cPut); 1♂, Dukati (cPut); 1♂, Mirdita, leg. Winneguth (cPut); 2♂♂, Latif, Orosi (cPut); 1♂, Latif, Cukali (cPut).

Greece: mainland: 2♀♀, Grevenithion, 39°50N, 21°01E, 5.VI.1975, leg. Malicky (cPut); 1♂, Ladikon, 38°42N, 21°40E, 23.V.1987, leg. Malicky (cPut); 2♂♂, 1♀, Sérres, Hagiai Ioannis, moss, 17.VIII.1964, leg. Puthz (cPut); 1♀, Penday, 38°35N, 22°04E, 3.VI.1975, leg. Malicky (cPut); 1♂, Iti, below Peristeri, 38°51N, 22°10E, 500m, 11.VI.1987, leg. Malicky (cPut); 1♂, Timfristos, 2000m, 8.VII.1982, leg. Osella (cPut); 1♂, Voiotia, Levadia, moss, 4.IX.1964, leg. Puthz (cPut); 1♀, Pelion, 25.III.1981, leg. Wunderle (cWun); 1♂, Pangéo, 26.VII.1988, leg. Jäch (cPut).

Pelopónnisos: 3♂♂, 2♀♀, Erimanthos, above Kalendzi, 37°57´02N, 21°46´34E, 1200m, stream bank, 27.III.1997, leg. Wunderle, Assing (cWun, cAss); 3♂♂, 2♀♀, 8km NE Kalavrita, bank of Vouraikos river, 38°04´34N, 22°09´43E, 700m, 30.III.1997, leg. Assing (cAss); 4♂♂, 7♀♀, Parnon range, 1100m, spring, wet moss, 13.VI.1996, leg. Wunderle (cWun, cAss); 2♂♂, Lakonía, Parnon, Polidroso, NE Sparti, 37°10´29N, 22°36´02E, 990m, waterfall, wet moss, 19.IV.1998, leg. Zerche (cAss). **Levkás:** 1♂, Vafkeri, 450m, 26.IX.1993, leg. Assing (cAss). **Andros:** 1♂, 1♀, above Sarisa, 37°51N, 24°54E, 20.IV.1984, leg. Malicky (cPut). **Thássos:** 1♂, Potamias, 13.IX.1991, leg. Jäch (cPut). **Andros:** 1♀, N Andros, 37°51N, 24°56E, 12.VI.1979, leg. Malicky (cPut). **Samothráki:** 4♂♂, 6♀♀, near Kremniotissa church, 40°25N, 25°34E, 24.V.1987, leg. Malicky (cPut); 1♀, 3 km SE Tharma, 14.VI.1993, leg. Jäch (cPut). **Samos:** 1♀, W Karlovasi, 37°48N, 26°41E, 27.V.1979, leg. Malicky (cPut); 1♀, 2km NE Kalithea, 37°45N, 26°36E, 26.V.1979, leg. Malicky (cPut). **Skyros:** 1♂, 1km W Skyros, 28.IX.1992, leg. Jäch (cPut). **Ikaria:** 3♂♂, 5♀♀, W Chrisostomos, 37°35N, 26°13E, 2.VI.1979, leg. Malicky (cPut, cAss); 2♀♀, W Mileopon, 37°39N, 26°14E, 2.VI.1979, leg. Malicky (cPut). **Rhódos:** 1♂, Petaloudes, 17.V.1966, leg. Leiler (cPut); 2♂♂, Farfalle valley, 12.V.1970, leg. Cerruti (cPut); 1♂, Apollona, IV.1966 (cPut); 1♂, Salakos, 15.IV.1977, leg. Besuchet (MHNG); 1♀, Epta Pigai, 9.IV.1977, leg. Besuchet (MHNG); 2♂♂, 2 exs., Kolimbia, 24.IV.1973, leg. Besuchet (MHNG).

Ukraine: Crimea: 7♂♂, 5♀♀, Crimeas reserve, upper part of Katcha river, 800m, 10.V.2000, leg. Ivanov (cPut, cSch, cAss); 1♂, Baidar, leg. Knirsch (cPut); 3♂♂, 2♀♀, Iaila range, leg. Winkler (MHNG, cPut); 1♀, Simferopol (MHNG).

Turkey: Istanbul: 7♂♂, 1♀, Istranca Dağ near Demirköy, pass, 700m, 12.VII.1972, leg. Heinz (cPut); 1♂, Beykoz, 1902, leg. Cameron (cPut); 1♂, Şile, 19.V.1987, leg. Schönmann & Schillhammer (cPut); 1♂, 1♀, Kilyos (=Kumkoy), 27.VII.1969, leg. Besuchet (MHNG). **Bolu:** 1♂, forest between Bolu and Yiğilca, 1100m, 18.VI.1987, leg. Heinz (cPut); 5♂♂, 7♀♀, Konuralp-Akçakoca, 400m, 15.V.1976, leg. Besuchet & Löbl (MHNG, cPut); 1♂, Ömerler near Bolu, 800m, 21.V.1976, leg. Besuchet & Löbl (MHNG). **Gümüşhane:** 1♂, Torul, 9.VI.1994, leg. Scoupý (cFel). **Trabzon:** 1♂, Maçka, 1000m, VII.1971, leg. Schubert (cPut). **Adiyaman:** 5♂♂, Nemrut Dağı, Karadut, 14.-19.VII.2000, leg. Smatana (cSch, cPut, cAss). **Diyarbakir:** 3♂♂, 3♀♀, 61km S Bingöl, cave near partly subterranean river, 9.VII.1974, leg. Heinz (cPut, cAss). **Bitlis:** 1♂, S Tatvan, 1700-2000m, 21.V.-18.VI.73, leg. Schubert (cPut). **Hakkari:** 1♂, N Semdinli, 3.VI.1987, leg. Schönmann & Schillhammer (cPut). **Mersin:** 1♀, Hacıiskakli, 27.IV.1978, leg. Besuchet & Löbl

(MHNG). **Isparta:** 1♀, Anamasdağı, leg. Weirather (cPut). **Burdur:** 2♂♂, 1♀, Çeltikçi, 850m, 5.V.1975, leg. Besuchet & Löbl (MHNG). **Antalya:** 1♂, 3♀♀, 30km N Finike, W Catallar, 23.5.1991, leg. Schönmann & Schillhammer (cPut); 1♂, 2♀♀, SSW Antalya, Çiralı, 36°25´N, 30°28´E, stream bank, 04.IV.2002, leg. Assing & Wunderle (cAss, cWun); 1♀, 3 km W Çiralı, 36°25´27N, 30°26´41E, 71m, stream bank, 28.III.2001, leg. Rose (cRos); 1♂, E Kumluca, 36°21´50N, 30°22´27E, 385m, stream bank, 3.IV.2002, leg. Assing & Wunderle (cAss); 1♀, same data, but 25.III.2002 (cAss); 1♂, N Kumluca, Altinyaka, 24.5.1991, leg. Schönmann & Schillhammer (cPut); 1♂, E Antalya, S Akseki, Topraktepe, 30.V.1983, leg. Brachat (cPut); 2♂♂, 1♀, Alanya, Kuzyaka, 180m, stream bank, 12.III.2000, leg. Rose (cRos); 1♂, 2km NW Antalya, 36°31´23N, 30°00´43E, 795m, moist locality with gravel, under bridge, 26.III.2001, leg. Rose (cAss); 2♂♂, 2♀♀, Catallar, 36°29´13N, 30°04´56E, 370m, stream bank, 26.III.2001, leg. Rose (cRos); 1♂, 1♀, 5km E Büyükalan, 36°43´29N, 30°21´13E, 1352m, roadside, near stream, 27.III.2001, leg. Rose (cRos, cAss); 1♂, 1km N Sögütcumavi, 36°41´51N, 30°22´30E, 1463m, stream bank, 29.III.2001, leg. Rose (cRos); 1♀, N Sagırın, Koprülü Canyon, 37°04´37N, 31°13´56E, 30m, stream bank, 17.III.2002, leg. Rose (cRos); 1♀, 5km NW Kemer, 36°36´03N, 30°29´04E, 197m, river bank, 30.III.2001, leg. Rose (cRos). **Muğla:** 1♂, Baba Dağ ["Salbakos Gbg."], leg. Weirather (MHNG). **Izmir:** 1♀, Izmir (MHNG).

Comparative notes: *Stenus maculiger* can be distinguished from *S. anatolicus*, *S. erythrocnemus*, and related species by a completely different shape of the aedeagus (shape and internal structures of median lobe, parameres extending distinctly beyond apex of median lobe, by the presence of a (sometimes very weak or indistinct) median furrow on the pronotum, the much lighter basal halves of the femora, and by the absence of antero-lateral pronotal tubercles (usually absent also in *S. cypriacus* and *S. prominens*). *Stenus sacrimontis* Puthz and *S. bosnicus* Bernhauer have an aedeagus of highly distinctive shape and with completely different internal structures; for illustrations see PUTHZ (1970b).

Distribution and intraspecific variation: As is illustrated in Map 3, *S. maculiger* is a typical example of a Ponto-Mediterranean faunal element. Based on a study of the internal structures of the aedeagi of specimens from various regions, two morphs were recognized, the distribution of one of them ranging from the southeast of Central Europe to Ukraine, southern Greece (including many islands), and Northern Anatolia, and that of the other confined to southern Anatolia (Map 3). The former morph has an aedeagus with an apically long and slender basal structure (Fig. 8, left); in addition, the elytra are often short and only slightly wider than the pronotum, and the hind wings are frequently of reduced length. In the latter morph, in contrast, the basal internal structure is apically stouter and shorter (Fig. 8, middle), the elytra are always distinctly wider and longer than the pronotum, and the hind wings are fully developed. One of the dissected males from Antalya (southern Anatolia), however, was found to have an internal structure (Fig. 8, right), which is apically almost as long and slender as in males e.g. from Greece, suggesting that the observed difference in the shape of the basal structure may not be constant. Both morphs may still represent species or subspecies, but in order to clarify the taxonomic status and rule out the possibility that the differences are merely an expression of intraspecific variation, more material especially from southern Anatolia must be examined.

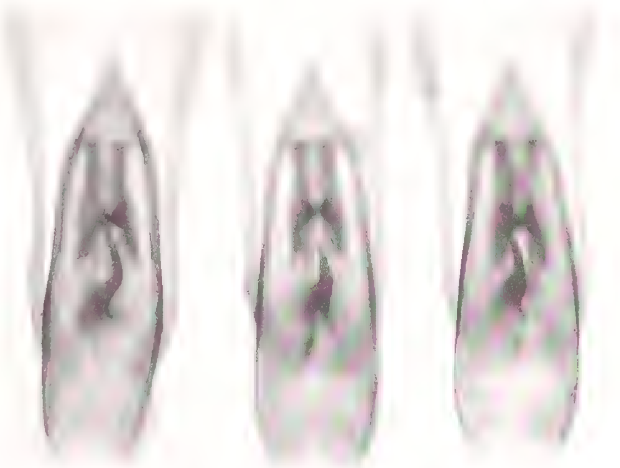
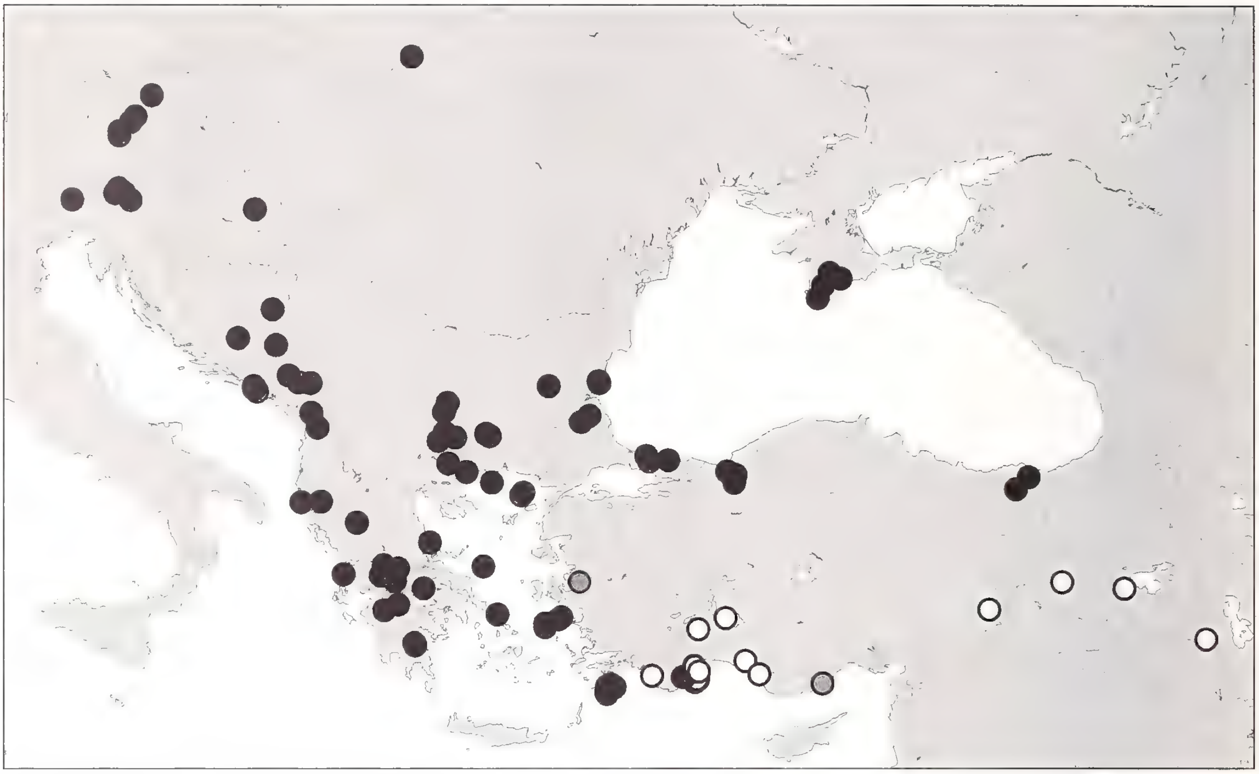


Fig. 8: *Stenus maculiger* Weise. Aedeagi of males from Greece (left) and southwestern Turkey (middle and right).



Map 3: Distribution of *Stenus maculiger* Weise, based on examined material, including four records from Austria examined and communicated to me by Volker Puthz. Filled circles: morph with long basal internal structure (Fig. 8, left); open circles: morph with short basal internal structure (Fig. 8, middle); grey circles: records represented only by females.

Acknowledgements. My thanks are due to all the colleagues indicated in the material section for the loan of material. In particular, I am grateful to Volker Puthz for several helpful discussions and for contributing unpublished data.

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Received:	28.06.2003
Accepted:	10.12.2004
Corresponding editor:	M. Schmitt

Bonner zoologische Beiträge	Band 53 (2004)	Heft 3/4	Seiten 311–321	Bonn, Dec. 2005

Reproductive Types and Mobility of Carabid Assemblages: Effects of Landuse Intensity of Extensively Managed Orchards

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Abstract. From April 1995 to November 1997 investigations were carried out in orchards (48.36N/9.23E): data were collected on the type and frequency of grassland use and on the carabid fauna. Seventeen sample plots were selected. Part of the plots had 25 years of unchanged management regimes: three-cutting meadows (3), two-cutting meadows (3), mulched meadows (4), abandoned meadows (3), a horse pasture, a sheep pasture with rotational grazing, a continuously grazed sheep pasture, and a sheep pasture abandoned in 1994.

A total of 68 carabid species was registered. Two-cutting meadows (20-24 species), three-cutting meadows (17-30 species), and pastures (16-27 species) showed a significantly higher diversity than mulched meadows (13-19 species), and abandoned plots (7-18 species). The diversity and activity densities on the studied plots decrease with lower land use intensity.

Reproduction: Spring breeders were more frequently found on sample plots than autumn breeders (63-87% to 12-38%) or species reproducing all year (0-11%). Increased shading by fruit trees lead to a decrease of the percentage of spring breeders.

Type of alae: The percentage of macropterous species was between 29 and 69%. Alae dimorphous species showed a percentage between 0 and 40%, and for brachypterous species the percentage was between 10 and 71%. The percentage of brachypterous species diminished along the land use gradient, while the percentage of alae dimorphous species increased.

Key words. Ground beetle, land use systems, mobility, reproductive types, species community.

1. INTRODUCTION

Vegetation and fauna of extensively managed orchards are mainly determined by the site and its maintenance, the type of grassland management and its land use intensity (DEUSCHLE et al. 2002). Until now animal assemblages of extensively managed orchards have not been analysed based on the direct comparison of different forms of grassland management. Forms like continuous and rotational grazing (sheep, horses) have not been taken into account. There are few investigations dealing with the influence of management systems on arthropod assemblages in extensively managed grassland, whereas the effects of grazing have been documented more frequently (HANSSEN & HINGST 1995; MAELFAIT et al. 1988; RUSHTON et al. 1989; SCHNITTER 1994).

Normally, orchards are regarded as ecologically high valid systems, but it is yet not known if and to what extent the management influences carabid assemblages. Is there an influence on the number of species or densities or on the capability for large or small species? Furthermore, it is asked whether resources are equal or randomly distributed in the orchard area or overwhelmed by the management regimes of the individual plots, thus the captured individuals show differences in their occurrence due to different management forms on the basis of their ecological characteristics.

Larval and adult hibernation are the two basic forms of reproductive strategies of carabids (autumn breeders, spring breeders). Differences in the reproductive strategies allow the carabids to live in spatial coexistence by exploiting the same resources at different times (MÜLLER 1987). Eurytopic woodland species are less dependent on specific reproductive forms (RODE 1993; OTTESEN 1996).

The capability of carabids to disperse is regarded as an important prerequisite for the survival of the species under frequently changing external conditions (DE VRIES et al. 1996). This holds especially true for the cultural landscape (DEN BOER & VAN DIJK 1994; RODE & DÜLGE 1994). It is known that macropterous individuals inhabit dynamic, continuously changing habitats in open cultural landscape. The species are often very small and have a high potential of dispersion for the colonisation of new habitats. But their populations are therefore exposed to a significantly higher risk of extinction (DEN BOER 1987; DINGLE 1996).

Brachypterous species are thought to have a smaller potential of dispersion. Especially eurotopic woodland species are brachypterous and in comparison they are quite mobile. From their original habitat they can migrate to explore and colonise suitable new habitats (GLÜCK & KREISEL 1986). Woodland species are regarded to be typical inhabitants of habitats with nearly constant living conditions. During the advancement of succession they are found more frequently in the spectrum of species (BUREL & BAUDRY 1994; POLLARD 1968).

So far the ecological characteristics of the species belonging to the carabid assemblage should be different if the beetles react to resources (GLÜCK & DEUSCHLE 2003). The capability of using the resources should then be reflected in their occurrence on different plots.

The aim of this investigation is to demonstrate how different management systems (meadows: two or three cuttings a year, pastures: continuous and rotational grazing with horses and sheep, mulched meadows, abandoned meadows) have influence on the mobility of the carabid assemblage. Mobile species should be more common under rapidly changing conditions like intensive mowing. It will be examined, if the reproductive strategies (spring breeders/autumn breeders) of carabid assemblages are influenced by the management system in specific areas. It will also be shown, which type of management favours brachypterous or macropterous individuals of certain species. The advantages and disadvantages of reproductive strategies and increased mobility will be discussed considering the small-patterned mosaic structure of extensively managed orchards with its inherit changing living conditions.

2. METHODS

2.1. Census and registration of land use in the orchards

From the beginning of April until mid October 1997 in the study area in the nature reserve "Limburg" (48.38N/9.23E, Fig. 1, Table 1), southwest Germany, the following parameters were recorded weekly or every two weeks: type of use, time of mowing, "mowing device", "whereabouts" of mowed grass, and number of grazing animals. The amount of ground shaded by trees under perpendicular solar radiation was estimated and assigned to the following categories (0, 1-20, 21-40, 41-60, 61-80, 81-100%). All areas, which are mowed completely on a regular basis every year and where the cut grass is removed, will be called "typical meadows". On "mulched meadows" the cut grass remains on the areas. "Continuous grazing" defines the management type of pastures, where the grazing animals can be found per-

Table 1. Morphology and land use of sampled plots

Plot	Land use	Type of land use	Area (Ar)	Circumference (m)	Altitude (mNN)	Shading (%)	Sampling period
3CM2	3-cutting meadow	meadow	26	209	405	20	`97
3CM3	3-cutting meadow	meadow	51	287	425	20	`97
3CM1	3-cutting meadow	meadow	16	204	392	20	´95,´96,`97
2CM3	2-cutting meadow	meadow	40	446	415	80	`97
2CM1	2-cutting meadow	meadow	10	218	445	60	´95,´96,`97
2CM2	2-cutting meadow	meadow	15	250	410	60	`97
SPA	abandoned sheep pasture (cont. grazing), see text	pasture	34	234	405	60	´95,´96,`97
SPC	sheep pasture (continuous grazing)	pasture	15	213	415	80	`97
HP	horse pasture	pasture	124	580	400	20	´95,´96,`97
SPR	sheep pasture (rotational grazing)	pasture	11	259	445	20	´95,´96,`97
MMI	mulched meadow (4 - 6 cuttings)	mulched meadow	12	162	455	20	´95,´96,`97
MME1	mulched meadow (3 cuttings)	mulched meadow	47	380	440	100	`97
MME2	mulched meadow (2 – 3 cuttings)	mulched meadow	29	217	420	60	´95,´96,`97
MME3	mulched meadow with 1 cutting	mulched meadow	25	206	517	80	`97
AMR	recently abandoned meadow (4 years)	succession	13	153	445	0	´95,´96,`97
AMO	old abandoned meadow (10 years)	succession	13	202	420	100	´95,´96,`97
WDL	woodland	succession	13	222	520	100	`97

manently on the same area, while “rotational grazing” is the type, where a particular area is grazed for a period of only a few days, but several times a year. Combinations of the three types of management forms can also be found in the extensively managed orchards of the nature reserve area. Management oriented ranking of plots on the basis of land use intensity was calculated (Table 2).

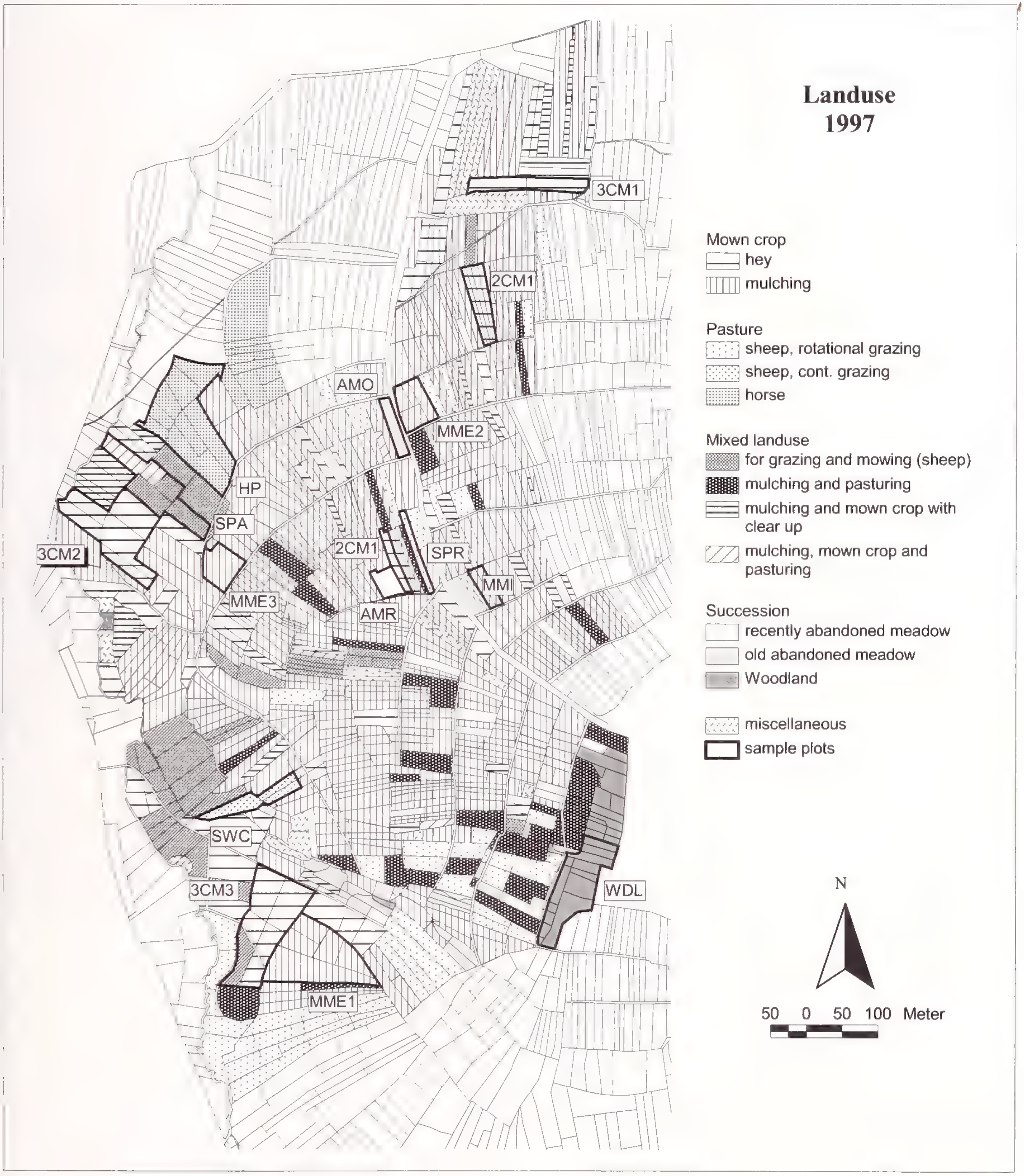
Landuse
1997
Mown crop
hey
mulching
Pasture
sheep, rotational grazing
sheep, cont. grazing
horse
Mixed landuse
for grazing and mowing (sheep)
mulching and pasturing
mulching and mown crop with clear up
mulching, mown crop and pasturing
Succession
recently abandoned meadow
old abandoned meadow
Woodland
miscellaneous
sample plots
3CM1
2CM1
AMO
MME2
HP
SPA
3CM2
2CM1
SPR
MMI
MME3
AMR
SWC
3CM3
WDL
MME1
N
50 0 50 100 Meter

Fig. 1: Land use intensity of grassland in the study area during the vegetation period of 1997.

Table 2. Management oriented ranking of plots. The column rank I scales exclusively the nine in 1995 to 1996 studied plots, rank II scales all studied plots in 1997 (see Figs. 2, 3)

Area plot	Rank I ('95/'96)	Rank II ('97)	Explanation
3CM2	-	2	
3CM1	1	2	From all plots here the strongest interference in the ecosystem appeared. Essential characteristic is a high biomass withdrawal in combination with comparatively frequent mowing.
3CM3	-	2	
2CM3	-	5	
2CM1	2	5	Same, however on a lower intensity.
2CM2	-	5	
SPA	-	7	The change in management from intensively pasturing in 1995/96 allows no clear allocation in the ranking. The up to now management as mowing pasture allows the position between the categories pastures and mowing meadows.
SPC	-	8	A nearly throughout the year intensively pasturing entails a high withdrawal of material during the vegetation period.
HP	3	9	In dry years the intensive pasturing leads to a high withdrawal of material during the entire vegetation period, whenever not only on etiolation spot a considerable part of the plant material is trampled down and therefore a further mulching is necessary.
SPR	4	10	During the yearly grazing, only a small part of biomass is removed, the larger part is trampled down by the animals and remains at the plot. The grazing corresponds to one mowing event on a mulching meadow.
MMI	5	11	On the whole area there is no withdrawal of biomass, but frequently mowing happens. The entire material is reduced to small pieces and remains until it is decayed as mulching layer on the soil surface.
MME1	-	12	Same, but with a lower cutting frequency (3x) and partly with a beam mower.
MME2	6	13	Same, but with a lower cutting frequency (2-3x) and partly with a beam mower.
MME3	-	14	Same, but with a lower cutting frequency (1x) and partly with a beam mower.
AMR	7	15	Since 5 years there is no withdrawal of material and no mowing.
AMO	8	16	Since 11 years there is no withdrawal of material and no mowing.
WDL	-	17	The area is at least 50 years out of management.

2.2. Selection of sample plots and population census of carabidae

In 1995 the selection of sample plots took into consideration areas which had been under the same management system for more than 25 years (Fig. 1, Tables 1, 2).

Six pitfall traps were placed in a single line 10 m apart on a transect through the centre of each sampling plot. Ethylene glycol (50%) was used as preservative solution, with detergent added to reduce surface tension. A cover made of Perspex (120 by 120 mm) was installed 30 to 50 mm above ground level. In 1995 (5 April to 1 November) traps were controlled and emptied regularly every week. In 1996 (5 May to 4 November) and 1997 (8 April to 4 November) the control interval was two weeks (DEUSCHLE & GLÜCK 2001).

2.3. Analysis of data and statistical methods

All registered data concerning management practices, vegetation, soil condition, and carabid population were integrated into a database. After examining the necessary conditions the following statistical tests were applied: U-test by Mann & Whitney (MWU-test), and chi^2-test. The rank correlation was calculated according to Spearman and the coefficients were tested on their significance.

3. RESULTS

3.1. Number of species and activity density of carabids

A total of 5229 beetles representing 68 carabid species were caught in pitfall traps during the three years of investigation. Eighteen species were caught only once. Regarding their mean number of species, meadows cut once or twice a year do not differ essentially from pastures. But all three management forms show a significantly higher number of species compared to mulched meadows or abandoned plots (Fig. 2). The number of species on the sample plots decreases with lower land use intensity. This trend is significant over all three years of investigation as well as for the cumulative number of species for the years 1995 to 1997. A decreasing density in the number of individuals along a gradient of land use intensity does not show a consistent annual tendency.

The activity densities of the sample plots for the years 1995 to 1997 show significant differences (Chi^2-Test, $p < 0.001$, $n = 9$). The mean densities of the number of individuals according to the management type do not differ substantially. Only three-cutting meadows show a tendency towards higher activity densities (Fig. 3, Table 3).

Table 3. Differences in mean number of carabid species and individuals on sampled typical meadows, mulched meadows, pastures, and abandoned meadows: Level of significance of paired MWU-tests (n.s. = not significant, * = $p < 0.05$, ** = $p < 0.001$, *** = $p < 0.001$)

	3-cutt. meadows (n = 5)	**2-cutt. meadows (n = 5)**	**Pastures (n = 10)**	**Mulched meadows (n = 8)**	**Areas under Succesion (n = 7)**	
3-cutt. meadows	-	n.s.	n.s.	p < 0,05	n.s.	
2-cutt.meadows	n.s.	-	n.s.	n.s.	n.s.	Number of Individuals
Pastures	n.s.	n.s.	-	n.s.	n.s.	
Mulch.meadows	p < 0,05	p < 0,01	p < 0,05	-	n.s.	
Areas and Suc.	p < 0,05	p < 0,01	p < 0,01	n.s.	-	
	Number of species					

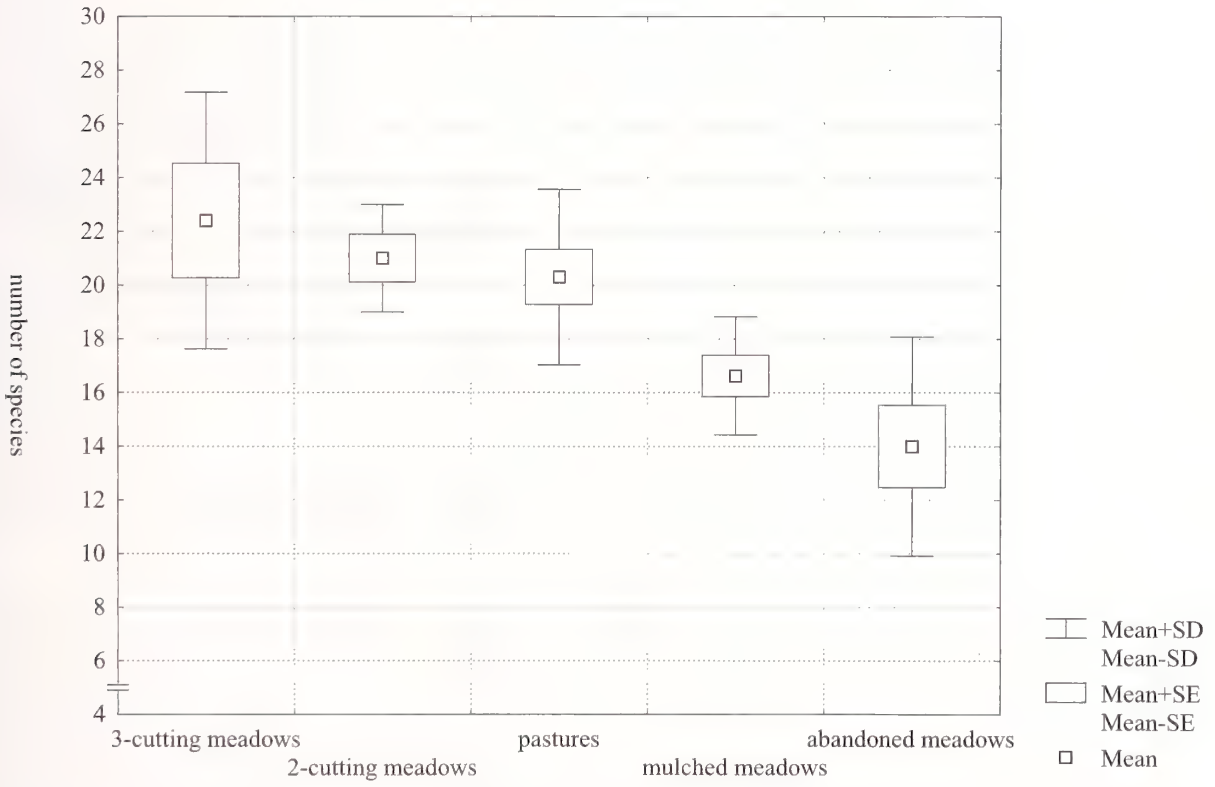

Fig. 2: Mean number of carabid species on sampled two-cutting and three-cutting meadows (each n = 5), pastures (n = 10), mulched meadows (n = 8) and abandoned meadows (n = 7), SE = standard error, SD = standard deviation.

3.2. Reproductive types

The highest percentages of adult hibernators were found on meadow 3CM1 (1995: 87%, 1996: 86%) and on the mulched meadow MMI (1995: 84%). The lowest percentages in 1997 responded to woodland (61%), as well as to the areas MME1 (62%) and 2CM3 (64%), and in 1996 to the mulched meadow MMI (64%). The areas which were sampled for three years showed differences in the yearly percentages between 2% and 14%. The smallest difference were registered on the horse pasture HP and on the mulched meadow MME2, the highest on the mulched meadow MMI (15%), the pasture SPR (14%), and on meadow 2CM1 (13%, Table 4).

Species reproducing the whole year – for example *Abax parallelepipedus* – were not found on pastures SPA, HP, and SPR during the whole investigation period, while on meadows 2CM1 and 3CM1, they were only detected in 1996. They were present on the mulched meadow MME2 and on the abandoned plots AMR and AMO in all three years. The only areas, which were sampled for the first time in 1997 and included reproducing species all year, were the plots 3CM3, 2CM3, SPC, MME3 and the woodland. This group had a low percentage of the total carabid assemblage, the highest appearing in 1996 on the abandoned plots AMR and AMO (14% and 15%, Table 4).

The reproductive strategies hardly seem to correlate with parameters like area, perimeter, and altitude of the sample plots. But the percentage of all-year reproduction types increased with decreasing land use intensity during the whole investigation. For the years 1995 and 1997 the correlation was significant (Table 5). The main reason was the high activity density of *Abax parallelepipedus*, as well as the lower number of typical carabids of extensively used open lands on mulched meadows and abandoned land.

In 1997 the percentage of spring breeders diminished significantly with decreasing land use intensity. A similar trend could not be detected for 1995 and 1996. It is also quite possible that the shading by fruit trees has an effect on the presence of spring breeders. During the three years of investigation the percentage of spring breeders decreased with increasing shading. The correlation is significant for 1997 (Table 5).

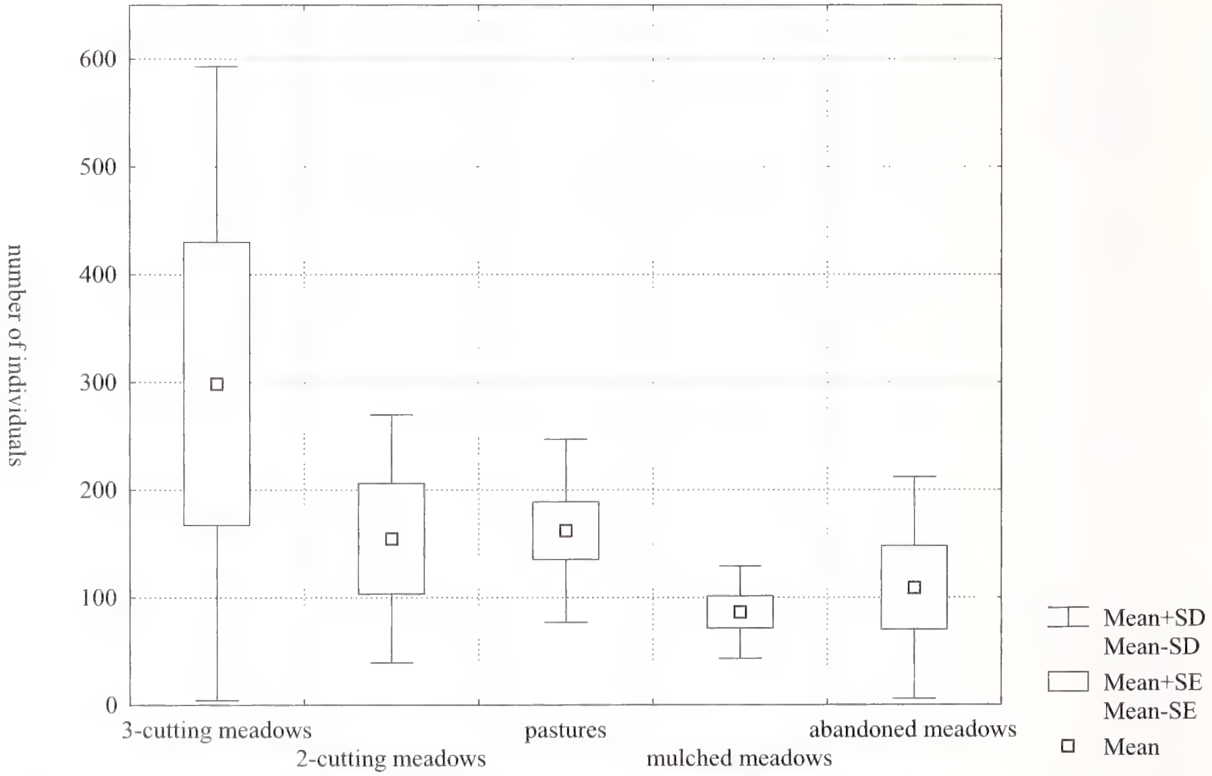

Fig. 3: Mean density of carabid individuals on sampled two-cutting and three-cutting meadows (each n = 5), pastures (n = 10), mulched meadows (n = 8) and abandoned meadows (n = 7), SE = standard error, SD = standard deviation.

3.3. Mobility and Dispersion

Forty of the total of 68 species caught in pitfall traps were macropterous and 16 were brachypterous species. Twelve additional species do not show a constant development of the alae and are therefore considered to be (alae) dimorphous. Brachypterous species are especially relevant, because their distribution is exclusively related to ground movement. The percentage of species in this group varied between 10% on sheep pasture SPA (1995 – 1997), and 71% on the abandoned plot AMO (1996). All meadows showed a smaller percentage. On pastures and mulched meadows it was generally higher. Especially on plot AMO, which was in a stage of succession, and in woodland, species of flightless carabids were quite frequent, while on the recently abandoned plot AMR few brachypterous species were found (Table 6).

In all three years the percentage of brachypterous species increased significantly with decreasing land use intensity. The smaller the perimeter of a sample plot, the less individuals of these species were found. On the other hand the percentage of alae dimorphous and completely macropterous species had the tendency to decrease with lesser land use intensity. In 1995 and 1996 the corresponding correlations for all flying species and in 1997 also for alae dimorphous species were high and significant (Table 7).

The alae morphology of all beetles caught was examined. Only *Bembidion properans* presented the macropterous and brachypterous forms (Table 8). Females were significantly more frequent than males (sex ratio 1:2.1 (m : f) MWU – Test $p < 0.05$). The sex ratio of macropterous beetles was 1: 3.2 (m : f). In the population of

Table 4. Dispersion strategies of carabids on sampled plots with different management regimes 3CM1, 2CM1, SPA, HP, SPR, MMI, MME2, AMR and AMO during the years 1995 to 1997 and 1997 only (species percentages)

		Macropterous	Dimorphous	Brachypterous
3CM1	1995	60.9	26.1	13.0
	1996	58.8	23.5	17.6
	1997	47.6	33.3	19.0
2CM1	1995	66.7	16.7	16.7
	1996	66.0	25.0	15.0
	1997	60.0	20.0	20.0
SPA	1995	55.6	33.3	11.1
	1996	60.0	30.0	10.0
	1997	40.0	35.0	25.0
HP	1995	50.0	31.8	18.2
	1996	45.0	40.0	15.0
	1997	58.3	25.0	16.7
SPR	1995	55.0	22.2	27.8
	1996	55.6	22.2	22.2
	1997	50.0	31.3	18.8
MMI	1995	52.6	21.1	26.3
	1996	43.8	25.0	31.3
	1997	56.3	25.0	18.8
MME2	1995	47.4	15.8	36.8
	1996	53.3	6.7	40.0
	1997	37.5	18.8	43.8
AMR	1995	52.9	17.6	29.4
	1996	58.8	11.8	29.4
	1997	50.0	25.0	25.0
AMO	1995	41.7	8.3	50.0
	1996	28.6	0	71.4
	1997	45.5	18.2	36.4
3CM2	1997	47.6	38.1	14.3
3CM3	1997	50.0	36.7	13.3
2CM3	1997	50.0	31.8	18.2
2CM2	1997	52.6	26.3	21.1
SPC	1997	55.6	25.9	18.5
MME1	1997	69.2	7.7	23.1
MME3	1997	52.6	21.1	26.3
WDL	1997	61.1	0.0	38.9

Table 5. Rank correlation coefficients regarding percentage of carabid species of different reproductive strategies with area parameter (1995/96: $n = 9$; 1997 $n = 17$; level of significance: * = $p < 0.05$, ** = $p <= 0.01$, *** = $p < 0.001$)

	Portion of species	Land use	Area	Perimeter	Altitude	Shading
1995	Spring breeders	-0,38	-0,58	-0,25	0,26	-0,54
	Autumn breeders	-0,15	0,56	0,76*	-0,38	0,56
	All-year reproductive	0,84**	0,05	-0,57	0,09	0,23
1996	Spring breeders	-0,09	0,04	0,10	-0,25	-0,56
	Autumn breeders	-0,20	0,10	0,27	0,19	0,20
	All-year reproductive	0,45	0,02	-0,53	-0,16	0,37
1997	Spring breeders	-0,65**	0,12	-0,19	-0,48	-0,70**
	Autumn breeders	0,31	-0,07	0,40	0,33	0,47
	All-year reproductive	0,64**	-0,10	-0,29	0,33	0,42

surveyed *B. properans,* females seem to be more alate than males. A total of 25% of all males and 38% of all females were macropterous. *Bembidion properans* was only detected on three-cutting meadows and pastures. But it was present on all plots of this type. Only a few macropterous males were caught on sheep pastures. The presence of *B. properans* on typical meadows and on the horse pasture was much higher. Females were found more frequently than males (Table 8).

4. DISCUSSION

Sixty-eight species of carabids were found on the sample plots under different conditions of land use intensity. The analysis of the reproductive types (adult hibernators, larval hibernators, and all year reproductive species) show that the percentage of spring breeders per plot decreases only slightly with diminishing land use intensity and shading (land use 1995: r_s= -0.38, 1996: r_s= -0.09, 1997: r_s=-0.65; shading 1995: r_s= -0.54, 1996: r_s= -0.65, 1997: r_s= -0.70). The corresponding correlation coefficients were significant in 1997 (Table 5).

Adult hibernators show declining numbers with decreasing land use intensity. This could be the result of less shading of more intensively used plots, which holds true not only for the sampling plots but for the entire area of investigation (Table 7). Therefore, the presence of adult hibernators does not depend on the type of management regime. An altitudinal moisture gradient does not seem to influence the distribution of spring breeders very much. Only for the year 1997 a decrease in the percentage of spring breeders can be detected with increasing altitude (Table 5). A significant increase in the percentage of all year reproductive species in 1995 and 1997 can be explained by the higher presence of the two woodland species *A. parallelus* and *A. parallelepipedus.* There does not seem to exist an overall tendency for the distribution of these reproductive types to be "driven" by land use intensity (FADL et al. 1998). The reproductive forms of both species are especially successful and present on areas without high interference (mulched meadows and areas under succession).

Table 6. Species percentages of reproductive types of carabids on sampled plots 3CM1, 2CM1, SPA, HP, SPR, MMI, MME2, AMR, and AMO during the years 1995 to 1997and 1997 only (Sb = spring breeders, Ab = autumn breeders, y = all-year reproductive)

		Sb	Ab	y
3CM1	1995	87.0	13.0	0
	1996	76.5	17.6	5.9
	1997	85.7	14.3	0
2CM1	1995	83.3	16.7	0
	1996	70.0	25.0	5.0
	1997	75.0	25.0	0
SPA	1995	66.7	33.3	0
	1996	75.0	25.0	0
	1997	70.0	30.0	0
HP	1995	77.3	22.7	0
	1996	75.0	25.0	0
	1997	75.0	25.0	0
SPR	1995	83.3	16.7	0
	1996	77.8	22.2	0
	1997	68.8	31.3	0
MMI	1995	84.2	15.8	0
	1996	62.5	37.5	6.7
	1997	68.8	31.3	0
MME2	1995	73.7	21.1	5.3
	1996	66.7	26.7	5.9
	1997	68.8	25.0	6.3
AMR	1995	82.4	11.8	5.9
	1996	82.4	11.8	14.3
	1997	75.0	18.8	6.3
AMO	1995	75.0	16.7	8.3
	1996	71.4	14.3	14.3
	1997	63.6	27.3	9.1
3CM2	1997	81.0	19.0	0.0
3CM3	1997	80.0	16.7	3.3
2CM3	1997	63.6	31.8	4.5
2CM2	1997	73.7	26.3	0.0
SPC	1997	74.1	22.2	3.7
MME1	1997	61.5	38.5	0.0
MME3	1997	73.7	21.1	5.3
WDL	1997	61.1	27.8	11.1

Table 7. Rank correlation coefficients of percentage of species regarding different dispersion strategies of carabid assemblage with area parameter (1995/96: $n = 9$; 1997: $n = 17$; level of significance: * = $p < 0.05$, ** = $p < 0.01$, *** $p < 0.001$)

	Portion of species	Land use	Area	Perimeter	Altitude	Shading
1995	brachypterous	0,91***	-0,17	-0,40	0,37	0,12
	dimorphous	-0,63	0,43	0,52	-0,43	-0,41
	macropterous	-0,76*	-0,26	-0,03	-0,02	-0,25
1996	brachypterous	0,82**	-0,20	-0,63	0,36	0,13
	dimorphous	-0,69*	0,25	0,54	-0,20	-0,21
	macropterous	0,63	-0,13	0,20	-0,11	-0,08
1997	brachypterous	0,74***	-0,28	-0,35	0,30	0,48
	dimorphous	-0,80***	0,29	0,13	-0,55	-0,57
	macropterous	0,17	-0,17	0,29	0,41	0,25

The removal of grass alters the ecological conditions on the surface and in the upper layers of the ground resulting in pronounced changes of temperature and moisture. On mulched meadows the cut grass remaining on the ground offers hiding places. It also serves as a buffer to weather changes during the following days and weeks. Therefore, the event of cutting grass has a much stronger effect on typical meadows than on mulched meadows.

Flightless (brachypterous) species colonise mulched meadows and areas under succession more often than typical meadows or pastures. On the other hand more flying (macropterous and alae dimorphous) species can be found on typical meadows and pastures (Tables 6, 7).

Mulched meadows do not seem to be barriers to brachypterous woodland species colonizing scattered areas under succession. During the three years of investigation the percentage of wingless woodland species was higher on mulched meadows and abandoned land than on typical meadows and pastures. Mulched meadows offer better resources to woodland species in spite of equal frequencies of mowing (BUTTERFIELD et al. 1995). Large forms of brachypterous woodland carabids, which are dependent on shade vegetation, have the tendency to look for shaded areas, if the contours of these areas stand out against their surroundings. It seems that a population can comprise parts of actively exploring individuals (direct movement vs random walk, see CHARRIER et al. 1997), which are capable of overcoming not optimal areas (BURKE & GOULET 1998; GARDNER et al. 1997; GLÜCK & KREISEL 1986). If they reach suitable habitats – in this case plots like AMO or MME2 – they can found new populations. Woodland species are especially dominant or sub-dominant on the abandoned plot AMO. Newly hatched individuals of *Abax parallelepipedus* and *Molops elatus* gave proof of successful reproduction of these species in area AMO.

Directed migration seems to be difficult under a closed canopy. The unshaded abandoned plot AMR, however, has a small percentage of woodland species. This is not typical for areas under succession and may be partly due to the influence of the neighbouring two-cutting meadow. Larger, eurotopic woodland species like *A. parallelus* and *A. parallelepipedus* were only found as single specimens during the investigation period. A growing number of woodland species could not be detected with increasing age of the abandoned area. On the heavily shaded mulched meadows MME2 and MME3 both species were more common (Fig. 3). Area AMR is lacking trees and dark contours. Both woodland species seem to frequent this area less.

Nearly all specimens of each of the nine alae dimorphous species were either completely macropterous *(Pterostichus vernalis, Synuchus vivalis* and *Stomis pumicatus)* or brachypterous *(Carabus granulatus, Calathus fuscipes, Pterostichus melanarius, Clivina fossor, Pterostichus anthracinus, Notiophilus palustris, Dyscirius globosus, Bembidion lampros).* They, therefore, showed a constant expression of the development of their alae. There were four wingless species found typical for three-cutting meadows *(C. granulatus, C. fuscipes, Pt. melanarius, C. fossor).* These ubiquitous forms were able to take advantage of the intensive use of grassland (TIETZE 1985).

In a pessimal environment the allele frequency of the corresponding recessive gene can increase within the population and minimize the risk of extinction (AUKEMA 1987, DEN BOER 1987). Dimorphous species also show numerous evidence of flight. The flight activity of both forms seems to be lower under high colonisation density (optimal conditions) than under low abundance (pessimal conditions, DESENDER 1986, MEIJER 1974). Numerous marked individuals of the small, eurytopic species *Calathus fuscipes,* which is alae dimorphous but mostly brachypterous, overcame larger distances on the ground than individuals of the larger, stenoecic and macropterous species *Harpalus dimidiatus.*

Table 8. Distribution and percentage of macropterous individuals of the alae dimorphous species *Bembidion properans* on sampled plots

Area	Sex distribution (%)		Macropterous (%)	
	males	females	males	females
3CM1 (1995-1997, n = 9)	44	56	22	22
SPA (1995-1997, n = 1)	100	0	100	0
HP (1995-1997, n = 15)	13	87	0	53
SPR (1995-1997, n = 1)	100	0	100	0
3CM1 (1997, n = 19)	26	74	0	26
3CM2 (1997, n = 16)	38	62	0	6
SPC (1997, n = 1)	100	0	100	0
Σ (n = 62)	32	68	25	38

The only species which included macropterous and brachypterous individuals was *B. properans* (Table 8). But the activity densities of this species were very low. Sheep pastures were colonised discontinuously by this species. A total of 63 specimens were caught during the investigation period. Male beetles were less alate than females, though they were present on more sample plots. Females were disproportionally more alate and less present, albeit the fact that their colonisation density was higher. Considering the reproductive behaviour of the species, females are more important. The ability to fly gives them the chance to leave an area when living conditions become pessimal. They can colonise other more profitable areas in a direct way and therefore minimize risk concerning their reproductive success. In the studied case this applies to three-cutting meadows and especially to the horse pasture. The high activity on this pasture corresponds with the findings of DESENDER & POLLET (1986), who describe an increase in the colonisation density of *B. properans* during intensified grazing. The radii of action of carabids stretch beyond the area defined by management practices. This leads to edge and spillover effects. Their dimensions depend on the individual mobility of the beetles, weather conditions, and availability of food.

For reproduction both strategies need nearly one year, especially the larval overwintering species can live for longer than one year and reproduce for more times (GRÜM 1976). The high loading variables of factor 1 show the meaning of the importance of mobility and therefore the possibility leaving areas with pessimal living conditions rapidly independent from reproductive success. Resulting adaptations to extreme disturbances as they occur in orchard by pasturing or mowing, are the most important influences for the distribution of carabid beetles. Different strategies of reproduction are less important. The fact that species can migrate into new habitats is well demonstrated (VAN DIJK 1987). A high mobility reduces extinction risk of pessimal living conditions and further more buffers the inter- and intraspecific competition by the larvae as well as in adult carabids. Mobility ensures and may maximize the reproductive success independent from the overwintering strategy.

Mowing and pasturing are the ancient practises of cultivating grasslands during the past few hundred years, on which the species corresponding could adapt themselves. No negative influence could be measured so long on carabid assemblages, because immediatelly after the impact higher or lower activities on the areas of investigation could not be measured (DESENDER et al. 1994) Obviously the impact is very grave and sustained for a long period. Only highly mobile species assemblages can profit from these living conditions.

But altogether only a combination of several factors might explain the distribution and composition of the assemblage.

Acknowledgments. We thank very much Dipl. Agr.-Biol. Ernst Rupp, Jutta Deuschle and Bradley Sinclair (ZFMK) for revising the English text.

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Received: 06.04.2004
Accepted: 15.09.2004
Revised: 04.04.2005
Corresponding editor: M. Schmitt

Bonner zoologische Beiträge	Band 53 (2004)	Heft 3/4	Seiten 323–332	Bonn, Dec. 2005

Rogambara and *Cabamofa*, Two New Genera of Enigmatic Sciaroids from Costa Rica (Insecta: Diptera: Sciaroidea)

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Abstract. In Costa Rica, two new species of peculiar sciaroids were found that are assigned to two new genera, *Rogambara dentata* gen. et spec. nov. and *Cabamofa mira* gen. et spec. nov. The new taxa are described, illustrated and their systematic relationships are discussed. Rogambara and Cabamofa appear to be sister groups and the two together are the sister group of *Ohakunea+Colonomyia.* All four genera form what is here called the *Ohakunea* group that is distinct from any of the existing families in the Sciaroidea and presumably closest to the Sciaridae.

Zusammenfassung. In Costa Rica wurden zwei bemerkenswerte, zu den Sciaroidea gehörige neue Arten gefunden, für die zwei neue Gattungen begründet werden: *Rogambara dentata* gen. et spec. nov. und *Cabamofa mira* gen. et spec. nov. Die neuen Taxa werden beschrieben, illustriert und ihre verwandtschaftliche Stellung wird diskutiert. *Rogambara* ist Schwestergruppe von *Cabamofa*; *Rogambara+Cabamofa* ist Schwestergruppe von *Ohakunea+Colonomyia.* Diese vier Gattungen bilden die so genannte *Ohakunea*-Gruppe, die keiner der existierenden Familien der Sciaroidea angeschlossen werden kann und vermutlich den Sciaridae am nächsten steht.

Key words. Phylogeny, taxonomy, new species

Stichwörter. Diptera, Sciaroidea, Phylogenie, Taxonomie, neue Gattungen, neue Arten, Costa Rica

1. INTRODUCTION

Fungus gnats in the broadest sense (Diptera: Sciaroidea) are poorly studied in Central America including Costa Rica, a fact applying absolutely to the species level and restrictively to all supraspecific levels. The preparation of the respective chapters for the Manual of Central American Diptera clearly meant a boost for systematic research on the Sciaroidea of this region, and one may hope that, once the Manual is published, this period of increased research activity and output will continue.

In the course of studies by the author on various groups of Costa Rican Sciaroidea, mainly Cecidomyiidae, Mycetophilidae and Sciaridae, two species of enigmatic sciaroids were found which could not be assigned to any of the existing family group taxa. Such 'unplaceable' sciaroids are usually rare, both in nature and collections. Moreover, they are much sought-after objects of phylogenetic studies aiming to further illuminate interfamilial relationships.

Detailed study of the two Costa Rican enigmatics showed that they belong to two different new genera, *Rogambara* and *Cabamofa*, that are closely related to one another and to two other 'unplaceable' genera, *Ohakunea* Tonnoir and Edwards, 1927 and *Colonomyia* Colless, 1963, with the last also present in Costa Rica (HIPPA & JASCHHOF 2004). These four genera together form what is here called the *Ohakunea* group. In the following, the new taxa are described, illustrated and their phylogenetic relationships are discussed.

2. MATERIAL AND METHODS

Specimens of the new species were picked from unsorted Malaise trap samples in the care of the Instituto Nacional de Biodiversidad (INBio), Santo Domingo, Costa Rica. It is noteworthy that only eight specimens in total were found among some 110 Malaise samples from various regions within this small but highly diverse country. Specimens were made transparent by treatment with KOH, dehydrated in ethanol and eventually, after treatment with beechwood creosote, mounted on microscopic slides in Canada balsam. All material, including types, are deposited in the INBio collection. Usage of morphological terminology follows that of SÖLI (1997) for Mycetophilidae. Drawings were made using an Olympus BX50 microscope in combination with the U-DA drawing unit.

3. TAXONOMY

3.1. Genus *Rogambara* gen. nov.

Type species. *Rogambara dentata* spec. nov., described below.

Description

Habitus: Slender, humpbacked sciaroids some 1.5 mm in size; moderately long antennae, legs and wings; rather narrow waist; slightly downcurved abdomen; and distinctive wing venation. Ethanol-preserved specimens coloration brownish.

Head: Head capsule higher than long; vestiture consisting of setae of various lengths, but short in all. Postfrons slightly bilobed, setose; frontal tubercle slightly two-pointed. Face larger than clypeus, non-setose. Clypeus setose, separated from face along its upper margin. Antenna shorter than body, little longer in females than in males, inserted slightly above midheight of head. Scape somewhat conical, subequal to subglobular pedicel, both setose. Antennal flagellum with 14 flagellomeres subequal in length, terminal flagellomere as long as or slightly longer than penultimate; each flagellomere cylindrical with very short conical neck and node less than twice as long as wide, neck and node weakly demarcated from another. Flagellum without microtrichia, except some basally on flagellomere 1. Each flagellomere with even cover of short setae arising from membranous rings and occurring in two sizes: fine and short setae, and stronger and longer ones arising from large basal pores, with latter more numerous in males than in females; setae interspersed with sensory spines; most proximal flagellomeres without setae arising from sockets (present in related genera); terminal flagellomere with 3-4 apical setae arising from sockets. Ocelli absent. Eyes reniform, with complete bridge at vertex, without interommatidal setulae. Mouthparts well developed, with short proboscis. Labrum sclerotized, triangular, non-setose. Maxilla with lacinia well developed, latter style-like and fringed terminally. Maxillary palpus with 3 segments, lacking "presegment"; first segment thickened, with densely set, long hyaline sensory hairs on inner side; second and third segments elongate; all segments setose with some setae spine-like. Labium with prementum (including premental apodemes) poorly developed, with strong setae. Labial palpus 2-segmented; labellum 1 smooth, with some setae; labellum 2 small, with some spine-like setae.

Thorax: Cervical sclerite well sclerotized. Antepronotum well developed, setose with 1 seta very long and strong; antepronotal sclerites interconnected by postpronotum forming very narrow ridge above neck. Episternum 1 clearly separated from pronotum, non-setose. Epimeron 1 small, subtriangular, situated at postero-ventral margin of episternum 1. Scutum with dorsal surface slightly evenly arched; with anterior parapsidal suture distinct and median transverse suture weak; with lateral, dorsocentral and acrostichal setae of various lengths, with some setae very long and strong. Paratergite distinct from scutum and well sclerotized. Scutellum setose, with 2 central setae very long and strong. Mediotergite in lateral profile high, slightly arched. Laterotergite large, pronounced, its ventro-anterior margin in touch with posterior margin of preepisternum 2, non-setose. Postphragma well developed, produced into abdominal cavity for about half length of first abdominal segment. Anepisternum 2 setose, large and elongate, subequal in length to preepisternum 2, both sclerites separated by distinct (anapleural) suture. Preepisternum 2 subtriangular. Pleural suture distinct. Pleural pit distinct. Epimeron 2 poorly sclerotized and demarcated, sometimes with anepimeral portion more distinct. Internal mid-coxal fork distinct. Metanotum poorly defined, forming narrow collar above mediotergite, with 1 long and strong seta on either side. Episternum and epimeron 3 both poorly sclerotized and demarcated. Openings of thoracic spiracles without striking features. **Legs:** Long, i.e. about 1.2 times length of body. Coxae moderately short, i.e. 0.6 (fore coxa) to 0.5 (hind coxa) times height of thorax. Femora slightly shorter than tibiae; tibiae shorter than tarsus. Tarsomeres 1-4 gradually decreasing in length, tarsomeres 1 more than twice as long as tarsomeres 2, tarsomeres 4 and 5 subequal in length. Coxae flattened, with long setae largely confined to anterior portions (fore coxa) or antero-distal margins (mid and hind coxae). Femora barely flattened, with longest setae (i.e., those along hind margins) clearly shorter than width of femur, with large non- and sparsely setose portions. Tibiae with tight cover of comparatively short setae interspersed with large trichia, the latter half to two-thirds as long as setae. Tibial spurs 1:1:1, comparatively long. Fore tibia with anteroapical depression delineated by indistinct subtriangular rim and bearing numerous setae in irregular (proximally) and comb-like (distally) arrangement. Hind tibia with subapical comb of stiff setae similar to those on fore-tibial depression. Vestiture on tarsi largely as on tibiae, additionally with 2 longitudinal rows of short, spine-like setae and 1 dense row of short, scale-like setae underneath. Pretarsal claws very small, slightly curved, without teeth. Empodia and pulvilli each consisting of some hairs shorter than claws. **Wing:** Clearly shorter than body, about 2 times as long as wide, widest near midpoint. No distinct alular or calypterous areas, anal area moderately developed. Membrane transparent, with light-brownish tinge, densely and evenly covered with microtrichia, without setae. Venation: C extending to apex of wing, near apex of M_1; Sc broad but very short, ending free; h broad but poorly demarcated; Rs pale, visible mainly through its tracheae, situated unusually close to wing base, with oblique inclination; R (i.e., vein portion between arculus and Rs) very short; R_1 (i.e., vein portion between Rs and junction point with anterior wing margin) excessively long, joining C near midpoint of wing; R_4 absent; R_5 (i.e., vein portion between diverging point of M_{1+2} and junction point with C which is clearly before wing apex) excessively long, almost straight; frm (i.e., vein portion between Rs and diverging point of M_{1+2}) present but extremely short; tb present but short and faint and visible mainly by its tracheae, with oblique inclination; mcu nearly absent; M_{1+2} furcate with stem and proximal portions of fork pale, with point where M_{1+2} diverges from R_5 very far basally and situated beyond Rs, fork clearly shorter than stem; origin of CuA_1 and CuA_2 closely approximated, i.e. forming fork without common stem; CuP broad, running close to and reaching half length of CuA_2; A_1 apparently running very close to CuP for some distance and thus indistinguishable; A_2 practically absent. Setae present along wing margin and ventrally and dorsally on R, R_1 and R_5. With number of sensory pores somewhat variable, i.e. on R_1, 1-2 distally, and R_5, 1-2 distally and 2-3 proximally, apart from numerous pores on Sc and stem vein. Halter club-shaped, with very few setae on both stem and knob.

Abdomen: Segments 1 and 8 shorter than other segments. Long, strong setae on all sclerites, except sternites 1 and 2. Number of spiracles uncertain. Tergal plaques small and inconspicuous, situated anterolaterally on each sclerite, with their pattern (as far as visible) 0/1-2/1/1/1/1/1/0. **Terminalia:** Male. Sternite 9 absent as distinct sclerite. Gonocoxites without lobes; gonocoxal apodemes broad. Gonostyli simple (i.e., not lobed), with apical tooth-like structure. Ejaculatory apodeme long, broad and flat, for most part poorly sclerotized. Parameres merged, i.e. forming a tegmen; dorsal parameral apodemes very short and interconnected by sclerotized transverse bridge. Tergite 9 large, plate-like. Tergite 10 absent. Cerci with numerous setae of various lengths distally and dorsally. Hypoproct consisting of one weakly sclerotized lobe, with 2 strong setae. Female. Tergite 8 large, sclerotized, setose. Gonocoxites 8 extended to proximal cercus, truncate terminally, with less than 10 strong setae distally and finer, shorter setae elsewhere; gonapophyses 8 distinct, weakly sclerotized; tergite 9 short, non-setose; gonapophysis 9 weakly sclerotized (i.e., not visible); tergite 10 well-developed but short, setose with some setae longer than any other setae on abdomen, with short posterior extension in which proximal cercus is embedded; sternite 10 present as weakly sclerotized ribs possibly merged posteriorly, with 1 strong lateral seta on either side; cercus one-segmented with distal segment absent; proximal cercus segment bearing numerous strong, straight setae, longer than wide, rounded posteriorly. Two sclerotized, disc-shaped spermathecae .

Immature stages. Unknown.

Diagnosis and discussion. The genus *Rogambara* is characterized by the following apomorphous characters: (1) the absence of ocelli; (2) the complete eye bridge; (3) the number of palpus segments reduced to three; (4) enlarged anepisterna 2; (5) the set of tibial spurs reduced to 1:1:1; (6) the basalization of wing veins; (7) simplified male terminalia; and (8) female terminalia with the distal cercus segments absent. Character 6 actually stands for a number of derived features following from the basalization of Rs (JASCHHOF & HIPPA 2003). Character 7 is actually a complex of characters, of which the most important are: the absence of a separate sternite 9; the absence of gonocoxal lobes; and the presence of a tegmen resulting from the fusion of the parameres. Characters 4 and 5 are truly autapomorphous characters of the genus *Rogambara* and found nowhere else in the sciaroids considered its closest relatives (see Phylogeny Section below).

Etymology. The genus name is composed of the family names of three of the parataxonomists working with INBio, Elias *Ro*jas, Billen *Gamb*oa and Wilfredo *Ara*na, in appreciation of their enthusiastic and productive work in the field. The gender is feminine.

***Rogambara dentata* spec. nov.** (Figs. 1-15)

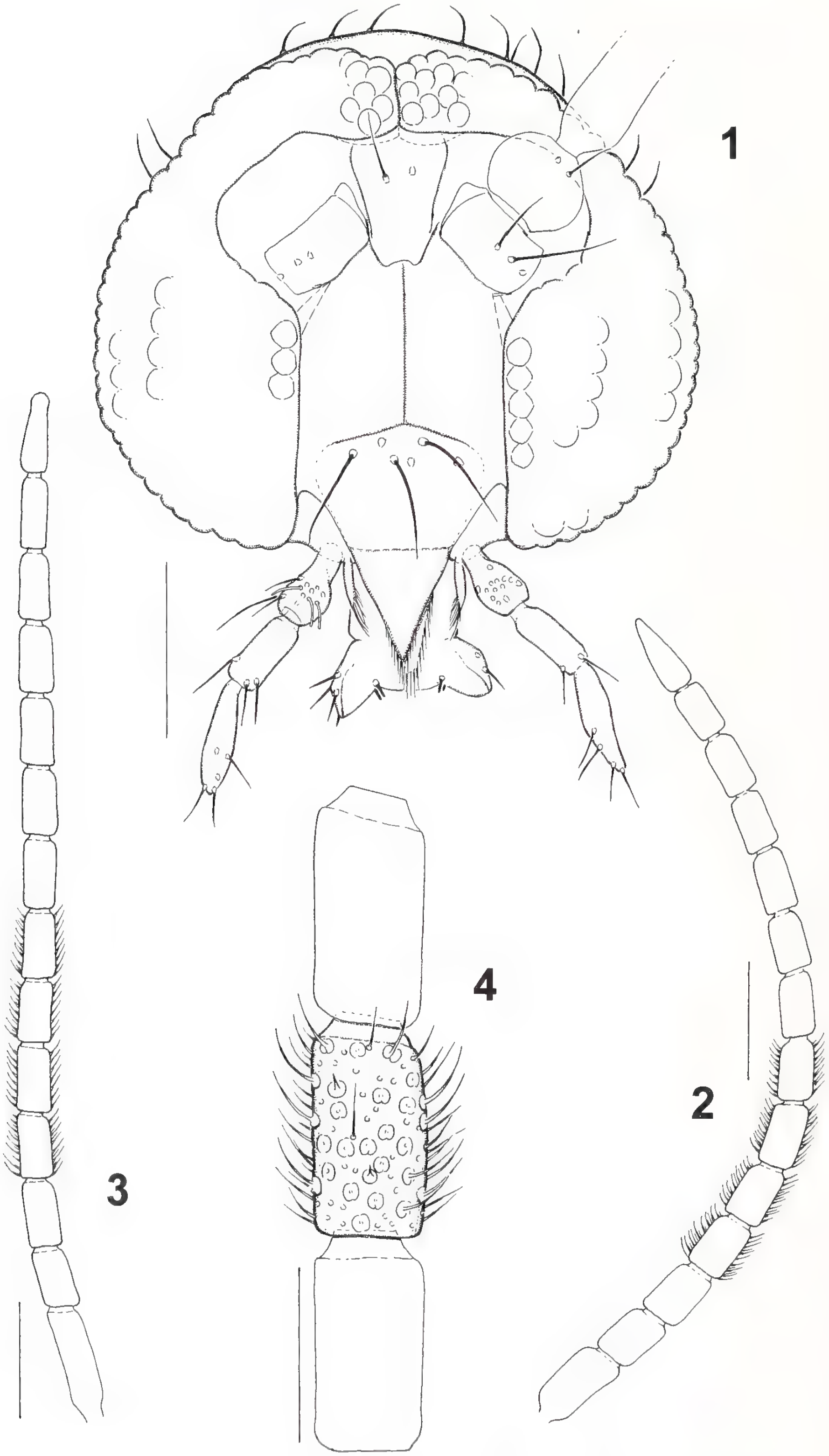
Types. Holotype: Male, Costa Rica, Prov. Limón, Reserva Biológica Hitoy Cerere, Sendero Espavel, 550 m, in tall secondary rain-forest, 18 Sept.-7 Oct. 2003, by Malaise trap, E. Rojas, B. Gamboa, W. Arana, M. & C. Jaschhof. **Paratypes:** 1 male, 2 females, same data as holotype; 1 female, same locality as holotype, but 11 March-1 April 2003; 1 male, Prov. Puntarenas, Parque Nacional Corcovado, 800 m Sendero a Cerro Rincón, 745 m, 20 Dec. 2001-7 Feb. 2002, by Malaise trap, J. Azofeifa.

Other material studied. Costa Rica: 1 male, Limón, Siquerres, Pacuarito, Los Brisas, Reserva Ecologica Rio Dantas, near Estacion El Palenque, 500 m, 22-26 August 1996, by Malaise trap, B. Gustafsson, T. Pape and B. Viklund (in Swedish Museum of Natural History, Stockholm). **Panama:** 1 male, Caribbean coast, San Lorenzo Protected Area near Colon (9°17`N, 79°58`W), wet evergreen forest, 130 m, 18 October 2003, by ground flight interception trap, A. Tishechkin (in Zoology Department, Canterbury University, Christchurch).

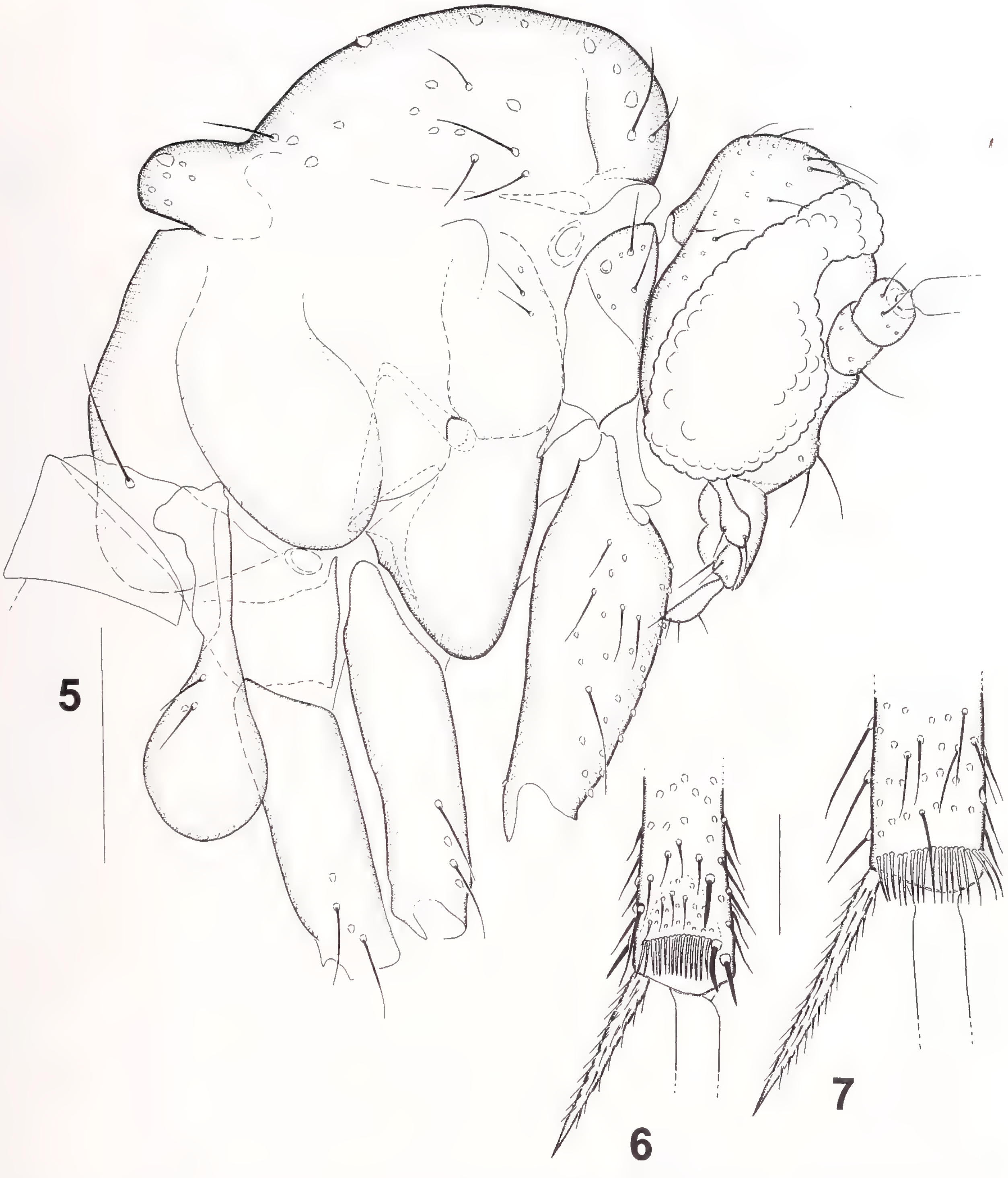
Description (for characters not mentioned here, see genus description above)

Body length: Males – 1.4 mm, females – 1.5-1.6 mm.

Male. Head: Postfrontal lobes each with 1 seta. Antenna (Fig. 2) with fourth flagellomere twice as long as wide, vestiture clearly shorter than width of flagellomere. Eye bridge at vertex 3 facets long. Labrum comparatively wide.



Figs. 1-4: *Rogambara dentata* spec. nov.; – 1: Head of female, frontal view (0.1 mm); – 2: Antenna of male, lateral view (0.1 mm); – 3: Antenna of female, lateral view (0.1 mm); – 4: Flagellomeres 3-5 of female, lateral view (0.05 mm). 1, 3 and 4: Paratypes from Hitoy Cerere; 2: Paratype from Corcovado (In parentheses: Length of scale bar.).



Figs. 5-7: *Rogambara dentata* spec. nov.; – 5: Head and thorax of female, lateral view (0.2 mm); – 6: Apical portion of fore tibia of male (0.05 mm); – 7: Apical portion of hind tibia of male (0.05 mm). 5: Paratype from Hitoy Cerere; 6, 7: Paratype from Corcovado (In parentheses: Length of scale bar.).

Thorax: Anepisternum 2 with maximum 6 setae in upper half. **Legs:** Fore tibia with anteroapical depression bearing comb of some 15 stiff setae (Fig. 6). Hind tibia with subapical comb of some 15 stiff setae (Fig. 7).

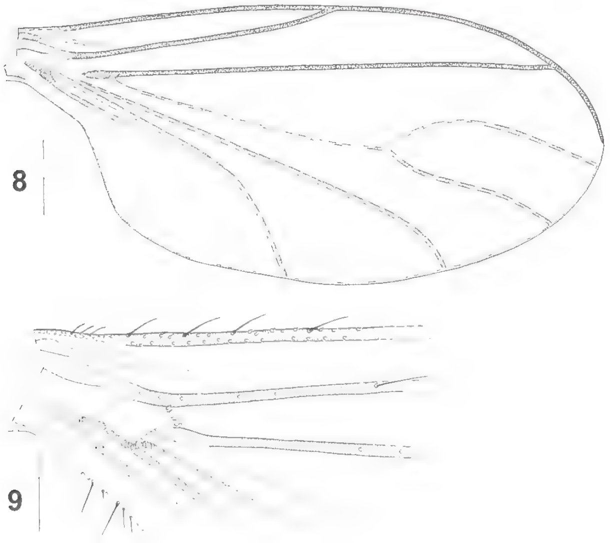
Terminalia: Gonocoxites (Fig. 10) ventrally with wide, V-shaped emargination, below emargination largely membranous and non-setose, with setae of various lengths elsewhere; gonocoxal apodemes broad and strong. Gonostyli (Fig. 10) tapering to tip; with heavy, curved tooth terminally and setae of various lengths elsewhere. Ejaculatory apodeme (Fig. 11) present as broad, flattened, weakly sclerotized rod almost as long as tegmen. Tegmen (Fig. 11) somewhat longer than wide, rounded distally; ventral gonocoxal apodemes swept ventrally; dorsal gonocoxal apodemes very short, interconnected by strong, short, sclerotized transverse bridge. Tergite 9 (Fig. 12) plate-like with long anterolateral bars and broadly rounded distal margin, with numerous setae of various lengths 2 of which are very long and strong. Cerci (Fig. 10) setose, large, broadly rounded terminally. Hypoproct (Fig. 10) consisting of smooth, rounded lobe bearing 2 strong setae.

Female. Head: See Figures 1, 5. Antenna as in Figure 3, with fourth flagellomere as in Figure 4.

Thorax: See Figure 5. **Wing:** See Figures 8, 9.

Terminalia: See Figures 13-15.

Etymology. The name is Latin meaning 'toothed', referring to the gonostylus tooth in males of this species.



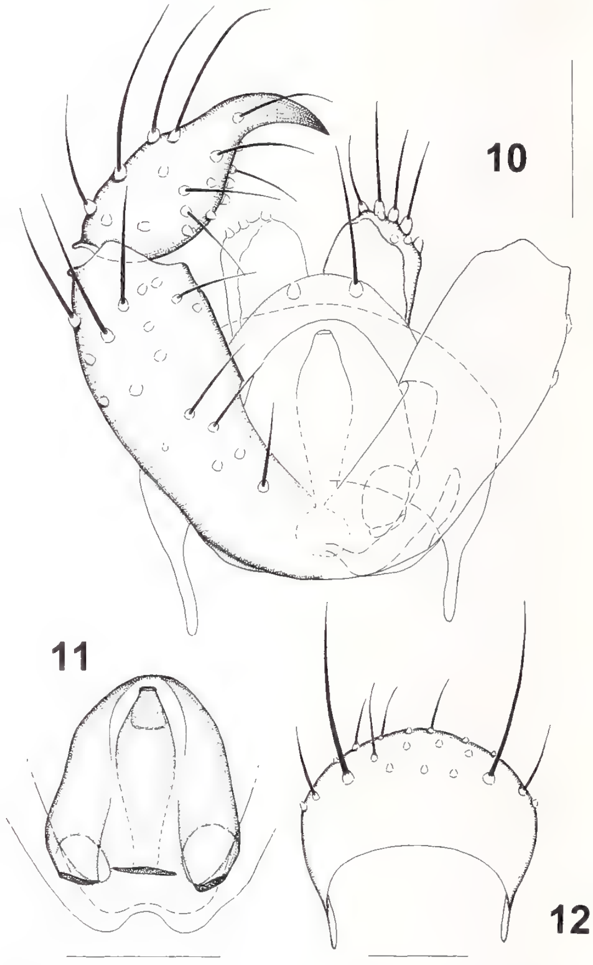
Figs. 8-9: *Rogambara dentata* spec. nov., paratype female; – 8: Wing, setae omitted (0.25 mm). – 9: Wing base (0.1 mm) (In parentheses: Length of scale bar.).

3.2. Genus *Cabamofa* gen. nov.

Type species. *Cabamofa mira* spec. nov., described below.

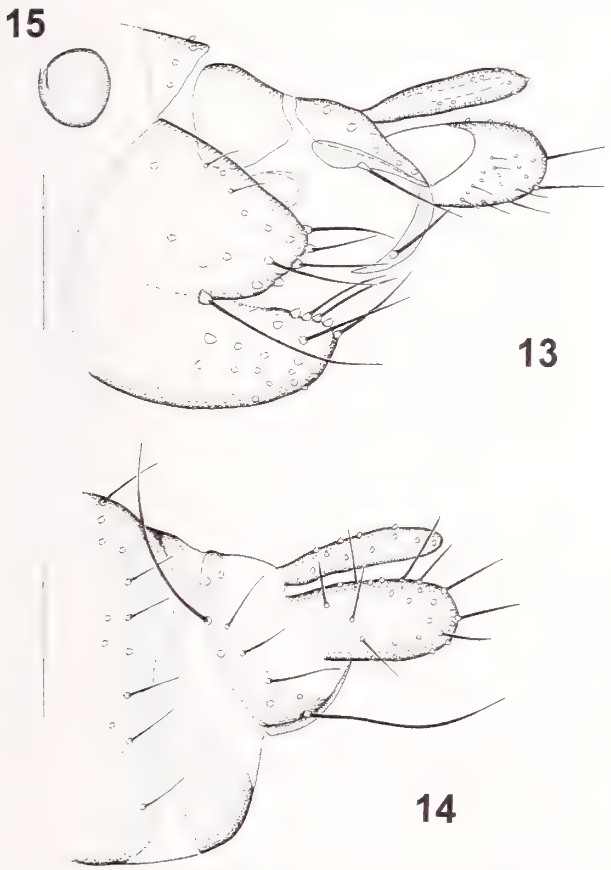
Description (based on females)

Habitus: Slender, humpbacked sciaroids some 3 mm in size (males might be considerably smaller); with moderately long antennae, legs and wings; rather narrow waist; and distinctive wing venation. Ethanol-preserved specimens coloration light-brownish.



Figs. 10-12: *Rogambara dentata* spec. nov., holotype male; – 10: Terminalia, ventral view; – 11: Tegmen and ejaculatory apodeme, ventral view; – 12: Tergite 9, dorsal view (Length of scale bar = 0.05 mm.).

Head: Head capsule subglobular; vestiture consisting of setae of various lengths, but short in all. Postfrons bilobed, non-setose; frontal tubercle slightly two-pointed. Clypeus setose. Antenna shorter than body, inserted slightly above midheight of head. Scape somewhat conical, subequal to subglobular pedicel, both setose. Antennal flagellum with 14 flagellomeres subequal in length, first and terminal flagellomeres clearly longer; each flagellomere cylindrical with short conical neck and node barely longer than wide, neck and node clearly demarcated from another. Flagellum without microtrichia, except some basally on flagellomere 1. Each flagellomere with irregular cover of long setae arising from sockets intermixed with short setae arising from membranous rings; setae interspersed with sensory spines. Ocelli absent. Eyes reniform, with complete bridge at vertex and long interommatidal setulae. Mouthparts well developed, with short proboscis. Labrum small, sclerotized, non-setose. Maxilla with lacinia well developed, the latter style-like and fringed marginally and terminally. Maxillary palpus with 5 segments including distinct "presegment" bearing at least 1 strong seta; third segment swollen, with sensory pit on inner side; fourth and fifth segments elongate; all segments setose with some setae spine-like. Labium with premental lobe bearing strong setae. Labial palpus 2-segmented; labellum 1 very small and non-setose; labellum 2 large, with spine-like setae in rows.



Figs. 13-15: *Rogambara dentata* spec. nov., paratype females; – 13: Terminalia, ventrolateral view; – 14: Terminalia, dorsolateral view; – 15: Spermatheca (Length of scale bar = 0.1 mm.).

Thorax: Cervical sclerite well sclerotized. Antepronotum well developed, setose; antepronotal sclerites interconnected by postpronotum forming very narrow ridge above neck and bearing setae laterally. Episternum 1 clearly separated from pronotum, setose. Epimeron 1 small, subtriangular, situated at postero-ventral margin of episternum 1. Scutum with dorsal surface evenly and slightly arched; anterior parapsidal suture distinct and median transverse suture weak; lateral, dorsocentral and acrostichal setae of various lengths. Paratergite poorly developed. Scutellum setose, with 2 central setae very long and strong. Mediotergite in lateral profile comparatively short, slightly arched. Laterotergite large, with rather smooth transition into mediotergite, its ventroanterior margin approximated with posterior margin of preepisternum 2, non-setose. Postphragma well developed, produced into abdominal cavity for short distance. Anepisternum 2 short, non-setose, both sclerites separated by distinct (anapleural) suture. Preepisternum 2 large, subtriangular. Pleural suture distinct. Pleural pit distinct. Epimeron 2 poorly sclerotized and demarcated. Internal mid-coxal fork distinct. Metanotum poorly defined, forming narrow collar above mediotergite, with 1-2 setae on either side. Episternum 3 large, weakly sclerotized, more clearly demarcated posteriorly with sometimes two parts recognizable. Openings of thoracic spiracles without striking features. **Legs:** Fore leg little shorter and hind leg little longer than body. Coxae moderately short, i.e. 0.6 (fore coxa) to 0.4 (hind coxa) times height of thorax. In fore leg, femur and tibia subequal in length, tibia shorter than tarsus. In mid leg, femur shorter than tibia, tibia shorter than tarsus. In hind leg, femur shorter than tibia, tibia and tarsus subequal in length. Tarsomeres 1-4 gradually decreasing in length, tarsomere 1 more than twice as long as tarsomeres 2, tarsomeres 4 and 5 subequal in length. Coxae flattened, with long setae largely confined to anterior portions. Femora barely flattened, with longest setae (i.e., those along hind margins) clearly shorter than width of femur. Tibiae with dense cover of comparatively short setae interspersed with large trichia, latter half to two-thirds as long as setae. Tibial spurs 1:2:2, comparatively short. In mid and hind tibiae, one spur clearly shorter than other. Fore tibia with anteroapical depression subtriangular, very weakly delineated, bearing numerous setae in irregular (proximally) and comb-like (distally) arrangement. Hind tibia with subapical comb of stiff setae similar to those on fore-tibial depression. Vestiture on tarsi largely as on tibiae. Pretarsal claws crescent-shaped, without teeth. Empodia well developed, as long as claws. Pulvilli delicate, two-thirds as long as claws. **Wing:** Shorter than body, more than 2 times as long as wide, widest slightly beyond midpoint. No distinct alular or calypterous areas, anal area moderately developed. Membrane transparent, with light-brownish tinge, densely and evenly covered with microtrichia, without setae. Venation: C extending to apex of wing, between apices of R_5 and M_1; Sc broad but very short, ending free; h broad but poorly demarcated; Rs pale, situated unusually close to wing base, with oblique inclination; R (i.e., vein portion between arculus and Rs) very short;

R_1 (i.e., vein portion between Rs and junction point with anterior wing margin) excessively long, joining C beyond midpoint of wing; R_4 absent; R_5 (i.e., vein portion between diverging point of M_{1+2} and junction point with C which is practically at wing apex) excessively long, curved in distal third; frm (i.e., vein portion between Rs and diverging point of M_{1+2}) present, longer than Rs; tb present, as long as one vein width; mcu present, pale, longer than Rs; M_{1+2} furcate with its stem almost entirely absent, point where M_{1+2} diverges from R_5 very far basally and situated clearly beyond Rs, fork clearly shorter than stem; CuA_1 and CuA_2 arising separately; CuP distinct, running close to and reaching beyond half length of CuA_2; A_1 extending to two-thirds length of CuP; A_2 nearly absent. Setae present along wing margin, ventrally on R, R_1, R_5, M-fork, CuA_1 and CuA_2, and dorsally on distal portion of R_5. Number of sensory pores somewhat variable, i.e. on R_1, 3-4; frm, 2-3; and R_5, 2 distally, apart from numerous pores on Sc and stem vein. Halter club-shaped, with setae on knob.

Abdomen: With segments 1 and 8 shorter than other segments. With setae on all sclerites except sternite 1. Number of spiracles uncertain. Tergal plaques apparently absent. **Terminalia:** Tergite 8 large, sclerotized, setose. Gonocoxites 8 extending up to proximal cercus, densely setose; gonapophyses 8 indistinct, weakly sclerotized; tergite 9 not recognizable as distinct sclerite, possibly merged with tergite 10; gonapophysis 9 present as internal sclerotized fork; tergite 10 setose, with posterior extension in which proximal cercus is embedded; sternite 10 not clearly recognizable; cercus two-segmented, setose; proximal segment subtriangular in lateral view, longer than distal segment; distal segment rounded. Two sclerotized, disc-shaped spermathecae .

Male and immature stages. Unknown.

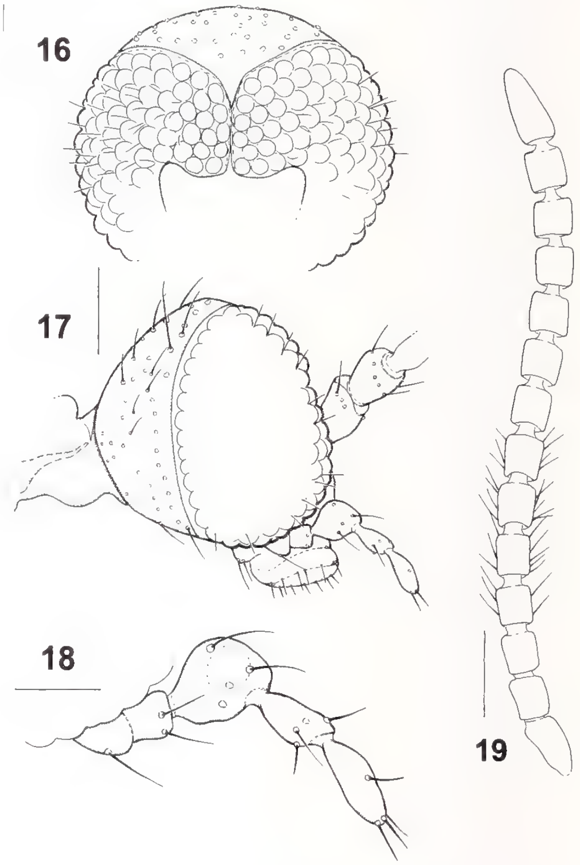
Diagnosis and discussion. In the genus *Cabamofa*, apomorphous characters include: the absence of ocelli; the complete eye bridge; and the basalization of wing veins. There is no autapomorphous character recognizable for *Cabamofa*; instead, all its derived features are found also in *Rogambara*. However, quite a number of derived features in *Rogambara dentata*, including two autapomorphies recognized, lack in *Cabamofa mira*, a fact making it problematic to argue that these two species are congeneric. In *Cabamofa*, the vestiture of the antennal flagellum includes an even cover with setae arising from sockets, a feature unique within the *Ohakunea* group (see Phylogeny Section below), but at present it is hard to tell whether this is of more than species-specific importance.

Etymology. The genus name is composed of the family names of three of the parataxonomists working with INBio, Khanaki *Caba*llero, Marco *Mo*ragá and Alejandro Azofei*fa*, in appreciation of their successful field work to that we owe these very peculiar flies. The gender is feminine.

Cabamofa mira **spec. nov.** (Figs. 16-26)

Types. Holotype: Female, Costa Rica, Prov. Puntarenas, Parque Nacional Corcovado, Quebrada Ceniza, 300 m, 14 March-5 April 2003, by Malaise trap, K. Caballero, M. Moraga & A. Azofeifa. **Paratypes:** 1 female, same data as holotype.

Description (for characters not mentioned here, see genus description above)



Figs. 16-19: *Cabamofa mira* spec. nov., female; – 16: Eye bridge, dorsofrontal view (0.1 mm); – 17: Head, lateral view (0.1 mm); – 18: Maxillary palpus, lateral view (0.05 mm); – 19: Antennal flagellum, lateral view (0.1 mm). 16: Holotype; 17-19: Paratype (In parentheses: Length of scale bar.).

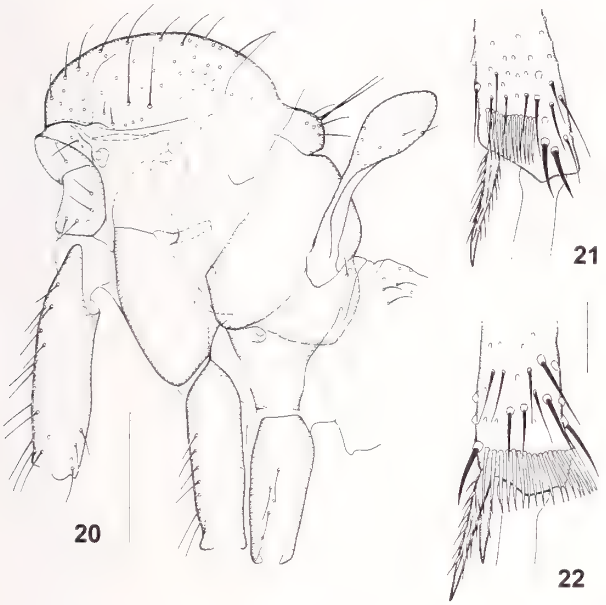
Body length: Females – 2.9 and 3.1 mm.

Male. Unknown.

Female. Head: See Figure 17. Antenna (Fig. 19) with node of fourth flagellomere (Fig. 23) 1.1 times as long as wide; longest setae shorter than width of flagellomere. Eye bridge (Fig. 16) at vertex 5 facets long. Maxillary palpus as in Figure 18.

Thorax: See Figure 20. Postpronotum with 3 setae laterally. Antepronotum with 1 seta. Episternum 1 with 4-5 setae. **Legs:** Fore tibia with anteroapical depression bearing comb of some 12 stiff setae (Fig. 21). Hind tibia with subapical comb of some 18 stiff setae (Fig. 22). **Wing:** See Figures 24, 25.

Terminalia: See Figure 26.

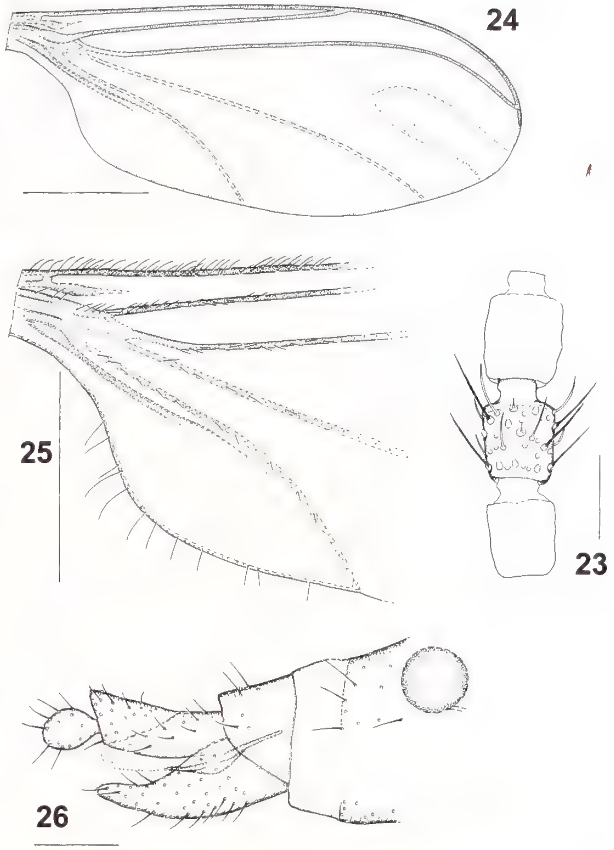


Figs. 20-22: *Cabamofa mira* spec. nov., holotype female; – 20: Thorax, lateral view (0.25 mm); – 21: Apical portion of fore tibia (0.05 mm); – 22: Apical portion of hind tibia (0.05 mm) (In parentheses: Length of scale bar.).

Etymology. The name is Latin meaning 'strange', referring to the peculiar assemblage of morphological characters in this species.

4. PHYLOGENY

The peculiar wing vein pattern and well developed postphragma in *Rogambara* and *Cabamofa* give reason to roughly assign them to a group of sciaroid genera which cannot be classified within any existing family of the Sciaroidea. Knowledge of these unplaceable sciaroids has increased significantly in recent years (see CHANDLER (2002) and JASCHHOF (2004) for *Heterotricha* Loew and allies; JASCHHOF & DIDHAM (2002) for Rangomaramidae; JASCHHOF & HIPPA (2003) for *Ohakunea* Tonnoir & Edwards; HIPPA & JASCHHOF 2004, for *Colonomyia* Colless); however, the phylogenetic relationships between these taxa and to the long-recognized family-level taxa within the Sciaroidea remain debatable.



Figs. 23-26: *Cabamofa mira* spec. nov., female; – 23: Antennal flagellomeres 3-5, lateral view (0.05 mm); – 24: Wing, setae omitted (0.5 mm); – 25: Wing base (0.5 mm); – 26: Terminalia with one spermatheca, lateral view (0.1 mm). 23, 24 and 26: Paratype; 25: Holotype (In parentheses: Length of scale bar.).

The basalization of Rs and other wing veins (Fig. 27, character 1) serves as an argument to consider *Rogambara*, *Cabamofa*, *Ohakunea* and *Colonomyia* belonging to the same monophyletic group, the *Ohakunea* group. *Rogambara* appears to be most closely related to *Cabamofa*. Postulation of their sister-group relationship is based on three arguments: the presence of a complete eye bridge, absence (loss) of ocelli and shortening of the antennal flagellum (Fig. 27, characters 2-4). As regards the last character, one must explain that shortening here means shortening of the individual flagellomeres, not shortening through reduction in the number of flagellomeres. The clade *Ohakunea+Colonomyia* is based on two synapomorphies: regaining of the R_4 and loss of sclerotized spermathecae (Fig. 27, characters 5 and 6). As argued by JASCHHOF & HIPPA (2003), R_4 was present in the ground plan of the Sciaroidea and later lost in the hypothetical common ancestor of a clade comprising Diadocidiidae, the *Heterotricha* group *sensu* CHANDLER (2002), *Ohakunea*, *Colonomyia*, Sciaridae, Rangomaramidae and Cecidomyiidae. Among the genera discussed here, *Rogambara* possessed the most apomorphous character states (Fig. 27, characters 7-10), which find their plesiomorphous counterparts in both *Ohakunea* (JASCHHOF & HIPPA 2003; and Fig. 27, characters 11-12) and *Colonomyia* (HIPPA & JASCHHOF 2004; and Fig. 27, characters 13-16). Among the derived features found in *Rogambara*, the three-segmented maxillary palpus and simplified male terminalia are most noteworthy as these correspond with the conditions found in the Sciaridae, a family considered most closely related to *Ohakunea* and *Colonomyia*. The structure of the maxillary palpus in *Rogambara* and Sciaridae is practically identical. As regards male terminalia, *Rogambara* and Sciaridae differ only in small details. The most important differences lie in the structure of the aedeagus/tegmen complex: in *Rogambara*, the ejaculatory apodeme is broad, flattened and as long as the tegmen and aedeagal teeth are absent; in Sciaridae, the ejaculatory apodeme is usually narrow, tube-like and shorter than the tegmen and aedeagal teeth are usually present. I explain the presence of a three-segmented palpus and simple male terminalia in both *Rogambara* and Sciaridae by homoplasy.

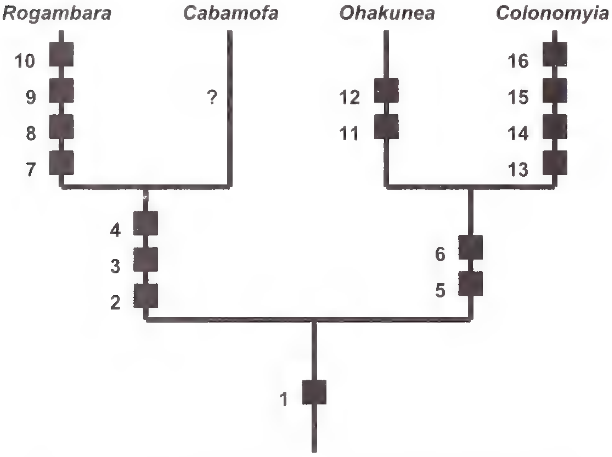


Fig. 27: Postulated relationships between the genera of the *Ohakunea* group (after JASCHHOF & HIPPA (2003); HIPPA & JASCHHOF 2004; and this study). Black blocks = apomorphous characters; ? = no apomorphy recognized. Numbers 1-16 refer to apomorphous character states as follows: 1, Rs and other wing veins basalized; 2, eye bridge complete; 3, ocelli lost; 4, antennal flagellum shortened; 5, R_4 regained; 6, sclerotized spermathecae lost; 7, number of maxillary palpus segments reduced to three; 8, anepisternum 2 enlarged; 9, one spur of mid and hind tibia lost; 10, male terminalia simplified; 11, male terminalia with parameres subdivided into ventral and dorsal pairs; 12, male terminalia with gonostyli strongly narrowed; 13, epimeron 2 shortened; 14, basitarsus with longitudinal row of specialized setae; 15, pretarsal claws deeply bifurcated; 16, male terminalia with gonocoxites bearing interior sclerotized ribs.

The absence of any autapomorphous characters in *Cabamofa* may be explained by the fact that its male is yet to be found, because experience shows that sciaroid male terminalia, due to their structural complexity, often can provide features of significance for phylogenetic considerations. No attempt was made in order to place the *Ohakunea* group among other Sciaroidea, as from a phylogenetic viewpoint the here introduced taxa cannot provide hints additional to those considered earlier (CHANDLER 2002; JASCHHOF & HIPPA 2003; HIPPA & JASCHHOF 2004).

Acknowledgements. Study of the insect collections at INBio was made possible through the generosity of INBio providing various support both in the laboratory and field during a three-month visit from September to November, 2003. In particular, I am much indebted to Manuel Zumbado for his attentiveness and interest, and to the parataxonomists Elias Rojas, Billen Gamboa and Wilfredo Arana who shared with us their knowledge on Costa Rican insects and wildlife. We thank the staff of the field station of the Reserva Biológica Hitoy Cerere facilitating greatly my four-weeks visit. My wife, Catrin Jaschhof, Greifswald, Germany, greatly assisted in the field and in sorting through numerous insect samples. Dr Raphael Didham, Zoology Department, Canterbury University, Christchurch, New Zealand, and Prof Dr Heikki Hippa, Swedish Museum of Natural History, Stockholm, Sweden informed me of material of *Rogambara dentata* in their collections. Language of the manuscript was kindly improved by Dr Bradley Sinclair, Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany. The helpful comments on the manuscript by two anonymous reviewers are gratefully acknowledged.

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Received: 02.03.2004
Revised: 10.05.2004
Accepted: 18.05.2004
Corresponding editor: B. J. Sinclair

Bonner zoologische Beiträge | Band 53 (2004) | Heft 3/4 | Seiten 333–357 | Bonn, Dec. 2005

The Net-Winged Midges (Diptera: Blephariceridae) of the Russian Far East

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Abstract. A revision and synopsis of the Diptera: Blephariceridae of the Russian Far East is presented; it includes generic keys to all life stages. Constitutive characters supporting the monophyly of the genera *Bibiocephala* Osten-Sacken and *Agathon* von Röder are named. Genera *Philorus* Kellogg and *Blepharicera* Macquart are recorded from the Russian Far East for the first time. New species described are *Philorus levanidovae* sp. n., *Blepharicera parva* sp. n. and *Agathon setosus* sp. n. The number of species known from the Russian Far East rises to eight. *Agathon decorilarva* (Brodsky, 1954), *A. eoasiaticus* (Brodsky, 1954) and *Neohapalothrix manschukuensis* (Mannheims, 1938) are widespread, ranging west to Mongolia and Kazakhstan, respectively, and *A. decorilarva* east to Kamchatka. All species were compared with actual specimens of close relatives from Korea and Japan and are distinct from them, except perhaps *Bibiocephala maxima* Brodsky, 1954. In the case of *Bibiocephala*, the world fauna is compared and keys to all stages of the four nominal species are provided. *Agathon kawamurai* (Kitakami, 1950) from Korea, *A. ezoensis* (Kitakami, 1950) from Sakhalin and Hokkaido, and the Korean *Philorus chosenensis* Kitakami, 1931 are redescribed from lectotypes, which are here designated.

Key words. Taxonomy, faunistics, new species, lectotype designation, keys, Far East Asia

1. INTRODUCTION

The Blephariceridae of the Russian Far East were first studied by BRODSKY (1954) who named several taxa. Unfortunately, Brodsky was apparently unaware of several studies by S. Kitakami who published on the Blephariceridae of Japan, Taiwan, Korea, Sakhalin, and Manchuria, from 1931-1950, and of the description of a peculiar Manchurian species (MANNHEIMS 1938). Two of Brodsky's taxa proved in the meantime to be synonyms of species named from nearby countries in the above papers. The validity of the remaining nominal species needed confirmation.

BRODSKY´S collection is in the Zoological Museum, St. Petersburg, but not all of his specimens could be located. Kitakami's collection in Kyoto (KITAKAMI 1951: 70) is apparently lost. Very few specimens remain in the Otsu Hydrobiological Station of Kyoto University at Otsu (K.N. Satake, in lit. 1987); we were unable to study them. However, Kitakami gave specimens in alcohol, including syntypes, to the United States National Museum (Washington, D.C.) and to B. Mannheims (Museum Koenig, Bonn, Germany). This material has uniform printed labels, occasional additions in ink are all in the same style, probably in Kitakami's own hand. A typed page by Kitakami sent to Mannheims lists every individual specimen with place and date of collection. The list shows that specimens belonging to some particular species and kept in the same vial may nevertheless have been collected at different places or times, respectively. Similar information is not available for the material in USNM. Therefore, even though the Washington specimens are authentic Kitakami material, they are eligible as lectotypes only under certain conditions, mainly taxa named in Kitakami's last taxonomical paper (1950) where all available specimens were listed as equal syntypes.

NARTSHUK (1999) presented keys to the then known larvae and pupae of the entire Russian fauna, to species or genus, respectively, apparently largely relying on published information. Adults were not considered.

2. MATERIAL, COLLECTION SITES AND DEPOSITORIES

During three weeks in June 1998, net-winged midges were the specific target of fieldwork by the authors and several of their colleagues in Primorye and the Khabarovsk district; collecting and treatment of collected insects conformed with Russian legal regulations. Whenever possible, large samples were collected to permit safe association of different life stages by dissection of pharate specimens, and to give an idea of the population structure at the time of sampling, and perhaps of volitinism and phenology. This alcohol-preserved material provides also information on habitat preferences and species associations. To avoid frequent repetition, locality information is gathered in Table 1.

Additional material collected by workers of the Institute of Biology and Soil Science, Academy of Sciences, Vladivostok (IBSSAN), consists of many smaller samples, most from the same general area. Some data were already published (AREFINA 1995). We list this addi-

Table 1. List of localities successfully sampled for Blephariceridae by the authors during field work in Primorye and the Khabarovsk District, in June 1998; material housed in coll. P. Zwick. Coordinates were read from Tactical Pilot Charts (prepared and published by the Defense Mapping Agency Aerospace Center, St. Louis, Missouri, 1986) and are approximate

RFE01	43°24'E, 132°48'N; Primorje, Steklyanukha River, tributary of Shkotovka River, Sevy Gorbatov Klyuch, waterfalls and cascades accessible from logging road beyond Novaya Moskva, 11.06.1998 and 26.06.1998
RFE03	43°03'N, 133°17'E; Primorje, Vodopadnaja River nr Nikolayevka, E of Partizansk [43.08N, 133.09E], 12.06.1998
RFE04	43°05'N, 133°18'E; Primorje, small rocky tributary to RFE03, at forest edge, 12.06.1998
RFE04	43°05'N, 133°18'E; Primorje, small rocky tributary to RFE03, at forest edge, 12.06.1998
RFE06	43°25'N, 133°28'E; Primorje, Povorotny River NE Partizansk [43.08N, 133.09E], on road to Lazo, 12.06.1998
RFE06	43°25'N, 133°28'E; Primorje, Povorotny River NE Partizansk [43.08N, 133.09E], on road to Lazo, 12.06.1998
RFE07	43°29'N, 133°42'E; Primorje, Lazovka River 30 km W of Lazo[43.25N, 133.55E], 12.06.1998
RFE08	43°28'N, 133°44'E; Primorje, Lazovka River 25 km W of Lazo [43.25N, 133.55E], at bridge, 13.06.1998
RFE09	43°12'N, 133°15'E; Primorje, Kiyevka River, 5 km S of Lazo [43.25N, 133.55E], 13.06.1998
RFE10	43°35'N, 134°36'E; Primorje, upper course of Milogradovka River, 25 km NW Milogradovo, 13.06.1998
RFE10a	Primorje, small forest tributary to RFE10 in forest, 14.06.1998
RFE12	43°38'N, 134°20'E; Primorje, Ussuri River, upper course on logging track from Margaritovka, N of pass, near Nishni, 15.06.1998
RFE13	43°42'N, 133°58'E; Primorje, Krasnaya River, tributary of Ussuri near Beryozovi, 15.06.1998
RFE14	43°43'N, 133°53'E; Primorje, Pravaya Poperechka River S of Arkhipovka, 15.06.1998
RFE15	43°53'N, 133°55'E; Primorje, Izvilinka River at Izvilinka, near mouth into Ussuri, 15.06.1998
RFE16	44°19'N, 133°54'E; Primorje, Ussuri River 6 km SW Kamenka, 15.06.1998
RFE17	44°41'N, 134°04'E; Primorje, Zadovka River, tributary of Zhuralyovka River 10 km SW Samarka, 16.06.1998
RFE18	44°43'N, 134°08'E; Primorje, Zhuralyovka River (tributary of Ussuri) at Samarka, 16.06.1998
RFE19	44°50'N, 134°19'E; Primorje, Komisarovski River near Lesogorje, tributary of Otkosnaya River/ Ussuri, 16.06.1998
RFE20	44°57'N, 134°24'E; Primorje, Malinka River S of Pozhiga, 16.06.1998
RFE21	45°05'N, 134°32'E; Primorje, Malinovka River ESE of Pozhiga, 16.06.1998
RFE22	45°06'N, 134°43'E; Primorje, cold forest tributary to RFE21, 3 km upstream on logging track, 17.06.1998
RFE23	45°26'N, 134°35'E; Primorje, Orekhovka River near Marevka, tributary Malinovka, 17.06.1998
RFE24	45°27'N, 134°42'E; Primorje, small tributary to RFE23, about 5km on, near Polyany, 17.06.1998
RFE25	45°28'N, 135°00'E; Primorje, small upper course of Orekhovka River, near pass to Perevalnaja River, 17.06.1998
RFE26	45°29'N, 135°04'E; Primorje, small forest stream just N of pass, Rogaty River, tributary of upper Perevalnaja River, 17.06.1998
RFE27	45°32'N, 135°04'E; Primorje, Rudny River, larger tributary of upper Perevalnaja River, 17.06.1998

RFE28	45°38'N, 135°10'E; Primorje, Perevalnaja River, near mouth of Dorozhny River, 17.06.1998
RFE30	46°32'N, 134°53'E; Primorje, branch of Bikin River near ferry, 25 km E of Verkhny Pereval, 18.06.1998
RFE31	Primorje, unnamed small stream on road, much disturbed through building of new culvert, turbid, 19.06.1998
RFE33	46°41'N, 135°27'E; Primorje, Bikin River and major tributary near Soboliny, 19.06.1998
RFE34	46°43'N, 135°28'E; Primorje, Stolbovaya River above Soboliny, tributary of Bikin River, 19.06.1998
RFE35	46°45'N, 135°33'E; Primorje, Tahalo River, large tributary to Bikin River at bridge, 19.06.1998
RFE36	46°48'N, 135°38'E; Primorje, Maly Tahalo River, 20.06.1998
RFE37	47°12'N, 135°34'E; Khabarovsky Kraj, Ivanov River at large bridge, between Yushnyi and Metsa, 20.06.1998
RFE38	47°22'N, 135°37'E; Khabarovsky Kraj, Dolmi River at Dolmi, S tributary of Khor River, 20.06.1998
RFE39	47°33'N, 135°33'E; Khabarovsky Kraj, Matai River, 20.06.1998
RFE41	48°04'N, 136°23'E; Khabarovsky Kraj, upper course of Nemtu River on road from Sidima to Sukpai, 21.06.1998
RFE42	Khabarovsky Kraj, small tributary to RFE41, about 3 km towards Sukpai, 21.06.1998
RFE43	48°05'N, 136°33'E; Khabarovsky Kraj, Petin River, tributary of Nemtu/Khor River, 21.06.1998
RFE44	48°02'N, 136°44'E; Khabarovsky Kraj, tributary to Ku River, 21.06.1998
RFE45	48°02'N, 136°44'E; Khabarovsky Kraj, cascades of small cold spring-fed stream 100 m uphill from RFE 44, 21.06.1998
RFE46	48°01'N, 136°46'E; Khabarovsky Kraj, Ku River, upper course at first bridge on road Sidima-Sukpai, 21.06.1998
RFE47	47°56'N, 136°46'E; Khabarovsky Kraj, Khor River below Sukpai village, 21.06.1998
RFE48	47°59'N, 136°47'E; Khabarovsky Kraj, Sukpai River at Sukpai village, 22.06.1998
RFE49	48°00'N, 136°53'E; Khabarovsky Kraj, large tributary to Sukpai River, 22.06.1998
RFE49a	48°00'N, 136°53'E; Khabarovsky Kraj, tributary to large tributary of Sukpai River, 22.06.1998
RFE50	47°47'N, 136°55'E; Khabarovsky Kraj, Sukpai River upper course at dead end of road, 22.06.1998
RFE52	Khabarovsky Kraj, Avan River on main road Khabarovsk – Vladivostok, just N of Kotikovo [47°27'N, 134°37'E], 23.06.1998
RFE53	Primorje, Bolshaya Ussurka, immediately above Dalnerechensk [45.55N, 133.43E], 23.06.1998
RFE54	44°45'N, 131°43'E; Primorje, Poperechnaya River, small tributary to Molokanka River W of Lake Khanka, 24.06.1998
RFE55	44°45'N, 131°52'E; Primorje, tiny trickle, tributary to Komissarovka River, at old bridge, 24.06.1998 (Kommissarovo [44.59N, 131,.46E])
RFE56	44°45'N, 131°48'E; Primorje, Komissrovka River, at mouth of Reshetinka River, SE of the Pogranichny Ridge, 24.06.1998
RFE100	43°21'N, 131°38'E; Gryaznaya stream, waterfalls, 10.07.1998, T. Arefina & T. Tiunova

tional material under the respective species only if taxonomically important, or if originating from places distinctly outside the range sampled in 1998.

We were also given valuable comparative material from Mongolia (P. Surenkhorloo, Ulan Bataar), Kazakhstan (V. Devyatkov, Ust-Kamenogorsk) and Japan (S. Uchida, Toyota). All of these collections are presently kept at Schlitz in collection P. Zwick (PZ) and will eventually be deposited in a public museum.

Comparative material was borrowed from the following collections: SAWL – Sächsische Akademie der Wissenschaften zu Leipzig, Arbeitsgruppe Limnologie, Lengfeld, Germany; USNM – United States National Museum, Smithsonian Institution, Washington, D.C., USA; ZFMK – Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany; ZIAS – Zoological Institute, Academy of Sciences, St. Petersburg, Russia

In lists of studied material, capital letters E, L, P stand for exuviae, larvae, and pupae, respectively. Larval instars 1-4 are identified by the respective numeral following the letter L.

3. KEY TO GENERA OF BLEPHARICERIDAE IN THE RUSSIAN FAR EAST

The Far East Russian fauna comprises five genera. Genus *Neohapalothrix* Kitakami is endemic to the eastern part of Asia, its closest relative being the European genus *Hapalothrix* Loew. The position of these genera in the family is doubtful – see under *Neohapalothrix* Kitakami. The other four genera belong to tribe Blephariceridni and exhibit amphi-Pacific disjunctions, with close relatives in western North America. In the Palaearctic Realm, *Bibiocephala* Osten-Sacken, *Agathon* von Röder and *Philorus* Kellogg are restricted to the eastern part of Asia, while *Blepharicera* Macquart is widespread in the northern hemisphere.

Adults

1 Branches of R on long fork (Figs. 1a-b) 2
1' Branches of R sessile, or from short fork (Figs. 1c-e) 3
2 An unconnected branch M_3 originating freely in wing membrane and ending in wing margin, and a basal crossvein between branches of M and Cu present (Figs. 1b) .... ***Philorus***
2' No unconnected vein in wing, no basal crossvein between M and Cu (Figs. 1a) .... ***Neohapalothrix***
3 R with three long branches, anterior branch ending in R_1 shortly before wing margin; basal crossvein between branches of M present (Fig. 1c) .... ***Bibiocephala***
3' R with two long branches; if a rudimentary anterior branch is present it ends in R_1 near base of latter and appears like an oblique crossvein forming a small triangular cell. Basal crossvein between branches of M present or absent (Figs. 1d, e) 4
4 Rudimentary branch R_2 delimiting small triangle present or absent; crossvein between M and Cu present (Fig. 1d) .... ***Agathon***
4' Neither rudimentary R_2 nor crossvein between M and Cu present (Fig. 1e) .... ***Blepharicera***

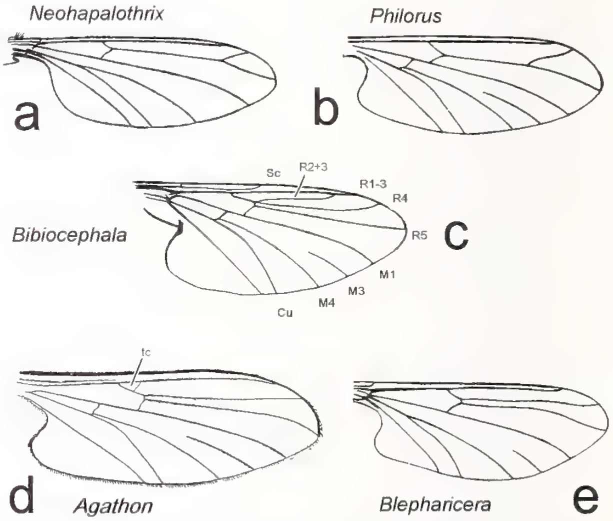

Fig. 1: Wing venation of Blephariceridae from the Russian Far East. a, *Neohapalothrix manschukuensis* (Mannheims) (after BRODSKY 1954); b, *Philorus asiaticus* Brodsky (after BRODSKY 1972); c, *Bibiocephala maxima* Brodsky (after BRODSKY 1954); d, *Agathon japonicus* (Alexander) (after KITAKAMI 1931); e, *Blepharicera asiatica* Brodsky (after BRODSKY 1976). Nomenclature of wing veins after HOGUE (1987); tc = triangular cell delimited on outside by R_{2+3}.

Pupae

1 Respiratory organs composed of four erect lamellae (Fig. 11); three or four pairs of abdominal adhesive organs 2
1' Respiratory lamellae in the form of short crests or flanges (Figs. 12d, e); three pairs of abdominal adhesive organs .... ***Philorus***
2 Respiratory lamellae resemble slender pointed triangles. Body cross-section approximately triangular, several abdominal tergites with median spines; four pairs of abdominal adhesive organs .... ***Neohapalothrix***
2' Respiratory lamellae tongue- or leaf-shaped, apices rounded; body cross-section rounded, regularly curved, no dorsal armature; three pairs of abdominal adhesive organs 3
3 Body highly domed, cross-section semicircular .... ***Bibiocephala***
3' Body moderately arched, cross-section lower than a half circle 4

4 All respiratory lamellae structurally similar, flexible. Dorsal surface matt, granulation strong, mesothorax with rugose zig-zag pattern .... ***Agathon***

4' Anterior and posterior respiratory lamellae hard, stiff, two inner ones soft. Dorsal surface shining, granulation fine and sparse, no zig-zag pattern on mesothorax .... ***Blepharicera***

Larvae (instars 2-4, with one to six filaments per gill)

1 Head capsule entire, posterior notches insignificant (Figs. 2a, c, 5) 2

1' Rear of head capsule laterally distinctly notched, usually deeply divided (to eye-spot; Fig. 12 f) 3

2 Antenna 2-segmented. Labrum sclerotized, forming part of a continuous prestomal ridge between left and right posterior mandibular articulations (Fig. 2b) .... ***Bibiocephala***

2' Antenna 3-segmented. Sclerotizations above mandibles extend between the two mandibular articulations on each side but are medially separated from each other by the soft labrum (Fig. 2c) ...... ***Agathon***

3 Body compact, abdominal segments lack "neck pieces". Highly convex, body cross-section triangular, dorsum of last instar with median row of spines. Two lateral pseudopods, both appressed to ground (L4), or single pseudopod forked (L3; Fig. 19e), or with knob (L2; Fig. 19d) .... ***Neohapalothrix***

3' Body not compact, abdominal segments 2-6 with narrow anterior portions (neck pieces), not highly arched, cross-section not triangular. Dorsal armature variable; if forming a median row it consists of blunt knobs or warts; dorsal pseudopods variable but never appressed to ground 4

4 Dorsal sensory pseudopod missing altogether, only ventral ambulatory pseudopod present (Figs. 16a, d). Dorsal armature, if any, consists of single blunt warts along midline .... ***Blepharicera***

4' Dorsal sensory pseudopod present, with dorsal process or erect spine; abdominal armature consisting of six structures per segment (Fig. 12 f) .... ***Philorus***

Larvae (first instar)

1 Dorsum with continuous transverse crests 2

1' Dorsum with transverse rows of separate erect little sclerites (Figs. 13, 19a, b) 3

2 Cephalic division with five crests, one on each thoracic and two on 1st abdominal segment .... ***Bibiocephala*** and ***Agathon***

2' Cephalic division with two crests (one on thorax, one on 1st abdominal segment) .... ***Blepharicera***

3 Dorsal sclerites are little triangular spikes arranged in transverse rows; cephalic division with four of these rows. Pseudopod with apical brush of slender setae (Fig. 13) .... ***Philorus***

3' Dorsal sclerites long and slender, band- or hair-like, in transverse rows; five of these on cephalic division. Pseudopod with group of retractile tiny hooks (Figs. 19a-c) .... ***Neohapalothrix***

4. TAXONOMY

4.1. Genus *Bibiocephala* Osten-Sacken, 1874

Bibiocephala Osten-Sacken, 1874. Type species: *Bibiocephala grandis* Osten-Sacken, 1874, by monotypy (OSTEN-SACKEN 1874: 564).

Amika Kitakami, 1950. Type species: *Liponeura infuscata* Matsumura, 1916, by original designation (KITAKAMI 1950: 37).

The genera *Bibiocephala* and *Agathon* were not separated by KITAKAMI (1931) but later he recognized their distinctness (KITAKAMI 1950). Unfortunately the nomenclature was confused; *Amika* Kitakami, 1950 is a synonym of the North American genus *Bibiocephala.* Kitakami erroneously used the latter name for what is in fact *Agathon*. Our present use of the name *Bibiocephala* is based on the redescription of the type species, *B. grandis* Osten- Sacken (HOGUE 1982) and conforms to the restricted use by HOGUE (1973, 1987) and ZWICK (1990, 1992).

Bibiocephala and *Agathon* differ from other northern hemisphere net-winged midges by characters in which they resemble the southern hemisphere Edwardsininae: undivided larval head capsule (Figs. 2a, c, 5); presence of a remnant of vein R_{2+3} (Figs. 1c, d), secondarily absent in individual species of *Agathon*; 4 visible growth zones of larval head capsule behind the cephalic sclerites, like in *Edwardsina* Alexander, 1920 (TONNOIR 1924; ZWICK 1977, fig. 22) and the Madagascan *Paulianina (Eupaulianina)* Stuckenberg, 1958 (STUCKENBERG 1958, fig. 28); *Philorus* also similar.

The first two agreements are undoubtedly plesiomorphic character expressions, the third probably so. Additional resemblances between *Bibiocephala, Agathon* and *Philorus* are difficult to interpret: dorsal larval pseudopods with erect outgrowth or process (Fig. 12f); in some species of *Agathon*, only a knob or angle remains; unique in the family; larval abdomen with six spines, sclerites or appendages standing in a characteristic arrangement (Figs. 8a, 12f); abdominal armatures are not uncommon in larvae of net-winged midges but in other taxa their arrangement differs.

In any case, the monophyly of the genera in question needs be established. As constituent apomorphies of genus *Bibiocephala* we accept the following characters:

Larva: Massive highly domed body (Fig. 2a). Mouth area forming a completely flat oral field surrounded in front by an essentially continuous triangular prestomal margin (Fig. 2b): Sides of prestomal margin formed by sclerotized arcs supporting mandibular articulations, the short transverse middle piece by the sclerotized, transversely folded labrum. Two setiform labral sensilla stand above, two below the sclerotized edge. In the groundplan of the family (for example, Fig.2c) the oral field is not flat and in front not surrounded by a continuous sclerotized prestomal margin because the labrum is largely soft and bulges forward and ventrad between the sclerotized arcs to its left and right which support the mandibular articulations. At the medial end, these sclerotized arcs turn dorsad towards the lower end of the median frontal sclerite.

Larva: Short stout lanciform or spatulate setae present on head in front of eyes, around antennal foramen, and on anterior corners of cephalic division (Fig. 5a; last instar only).

Pupa: Highly domed. Respiratory lamellae very large, often leafy.

Adult: Body unusually setose, especially males. Abdominal segment one fused to metathorax, tilted up, immobile; mobility of abdomen achieved via well developed membrane between abdominal segments one and 2.

♂: antenna short, compact; front femur arched; last tergite posteromedially sclerotized and spinulose.

♀: Pleuron and tergite 9 enlarged, both with fringe of dense, exceptionally long setae surrounding abdominal tip like a basket (see ZWICK 1990, fig. 1).

From the description by KITAKAMI (1931), the first instar larva of *Bibiocephala infuscata* has the full complement of transverse cuticular crests, that is, three thoracic and two abdominal ones on the cephalic division, and two each on the other abdominal segments. The pseudopod bears eversible hooklets.

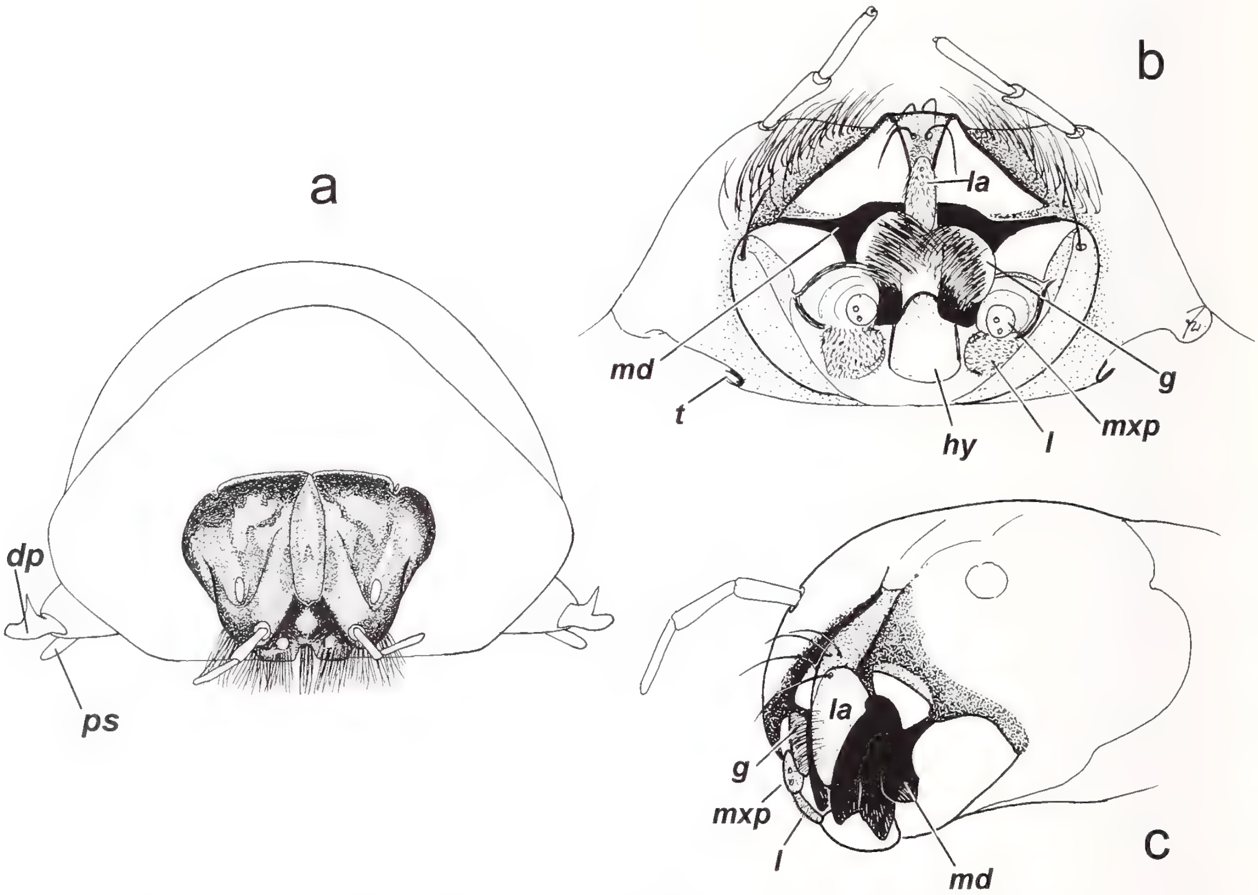

Fig. 2: a, *Bibiocephala grandis* Osten-Sacken, frontal view of last instar larva; b, *B. maxima* Brodsky, ventral view of head; c, *Agathon eoasiaticus* Brodsky, oblique frontolateral view of cephalic division, left antenna and maxilla removed. dp, dorsal pseudopod; g, galea; hy, hypopharynx; l, lacinia; la, labrum; md, mandible; mxp, maxillary palpus; ps, ventral pseudopod; t, tentorial invagination.

Nearctic *Bibiocephala* belong to a single species, *B. grandis* Osten-Sacken, 1874, which is widespread in western North America (HOGUE 1982). The number of Asian species is uncertain, see under *B. komaensis* Kitakami, 1950. We studied abundant material of *B. maxima, B. infuscata, B. grandis* as well as some larvae of *B. komaensis*. We summarise our knowledge in keys, which replace formal descriptions of the previously unknown larva of *B. maxima.* Keys also contain supplementary details on adults and pupae. There are excellent figures of male genitalia of *B. grandis* (HOGUE 1982, reprinted 1987) and of *B. infuscata* (KITAKAMI 1937), but dististyle structure of *B. maxima* in the existing figure (BRODSKY 1954) is confusing. We draw and compare the closely related Asian species (Figs. 3, 4), mainly to facilitate a decision on possible synonymy between *B. komaensis* and *B. maxima,* should fresh Korean material become available.

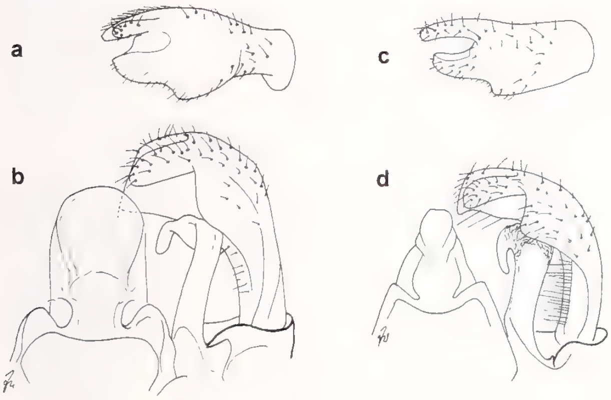

Fig. 3: *Bibiocephala infuscata* (a, b) and *B. maxima* (c, d). a, c, apical views of left dististyle; b, d, left dististyle and apex of tegmen in dorsal view. All to same scale.

4.1.1. Key to all known *Bibiocephala*-species

Adult males (*B. komaensis* (Kitakami) not known)

1 Hypopygium elongated, its anteroventral margin positioned much in front of anterior margin of tergite 9; anterior lobe of dististyle strongly spinose; inner dististyle with erect basal lobe on outside and simple band-shaped apex which is gently curved back; inner hypopygial sclerites partly rotated, penis filaments prolonged .... ***B. grandis*** Osten-Sacken

1' Hypopygium not elongated, anteroventral margin level with anterior margin of tergite 9; anterior lobe of dististyle finely pubescent; inner dististyle without basal lobe; inner hypopygial sclerites and penis filaments of normal length 2

2 Dististyle with massive apex, ventral lobe wide. In apical view, ventral lobe flat, much narrower than plump dorsal lobe; notch between lobes shallow, triangular (Figs. 3a, b). Apex of inner dististyle narrow, ribbon-like. Tegmen with broadly rounded spoon-shaped apex .... ***B. infuscata*** (Matsumura)

2' Dististyle slender, both lobes slender and narrow; in apical view, notch between them deeply U-shaped. Apex of inner dististyle narrow and pointed, semicircularly curved (Figs. 3c, d), surface before bend with curved rugosities. Apex of tegmen narrowed, tongue-shaped .... ***B. maxima*** Brodsky

Adult females (*B. komaensis* (Kitakami) not known)

1 Eyes almost meeting on vertex, ocelli on raised turret. Antenna shorter than head, beaded, flagellar segments two and following as long as wide, distal ones may be wider than long. Oviscapt ventrally with several large setae on bulging base, in addition to fine trichomes; laterodistal corners obtuse; paramedian tips with falcate sensilla barely visible in ventral view. Lobes covering dorsal side of oviscapt short, broadly divided, covered with stiff trichomes about as long as width of lobe (Fig. 4a). Seminal receptacles larger than oviscapt, basally gradually narrowed, coiled, eventually blending into long narrow duct .... ***B. grandis*** Osten-Sacken

1' Eyes widely separate on vertex, no ocellar turret. Antenna variable. Oviscapt without setae, only with fine trichomes; paramedian tips of oviscapt long, often partly visible in ventral view. Lobes covering dorsal side of oviscapt narrowly separated, stiff trichomes brush-like, much longer than width of lobe. Receptacles sharply set off against their short ducts (Figs. 4b, c) 2

2 Antenna longer than head plus rostrum, setiform, flagellar segments longer than wide. Laterodistal corners of oviscapt obtuse (Fig. 4c, d). Receptacles pyriform, about twice as long as oviscapt, surface of receptacles everywhere with fine pale punctures .... ***B. infuscata*** (Matsumura)

2' Antenna short, subuliform, basal flagellar segments wider than distal ones, only first flagellar segment longer than wide. Oviscapt with prominent laterodistal corners. Receptacles oval, about as long as oviscapt, (Fig. 4b) pale punctures only in basal half, distal half with fine dark trichomes inside .... ***B. maxima*** Brodsky

Pupae

1 Gills normal, the lamellae diverge only slightly; granula on pupal dorsum spinous .... ***B. grandis*** Osten-Sacken

1' Gill lamellae diverge strongly; pupal granula rounded 2

2 Gill lamellae spread out widely, slightly curled, suggesting a cabbage leaf. Wide margins of lamellae pale, covered with visible plastron .... ***B. infuscata*** (Matsumura)

2' Gill lamellae divergent but in regular alignment, one behind the other. Lamellae smooth, not curled, uniformly dark and shining, no plastron .... ***B. maxima*** Brodsky and ***B. komaensis*** (Kitakami)

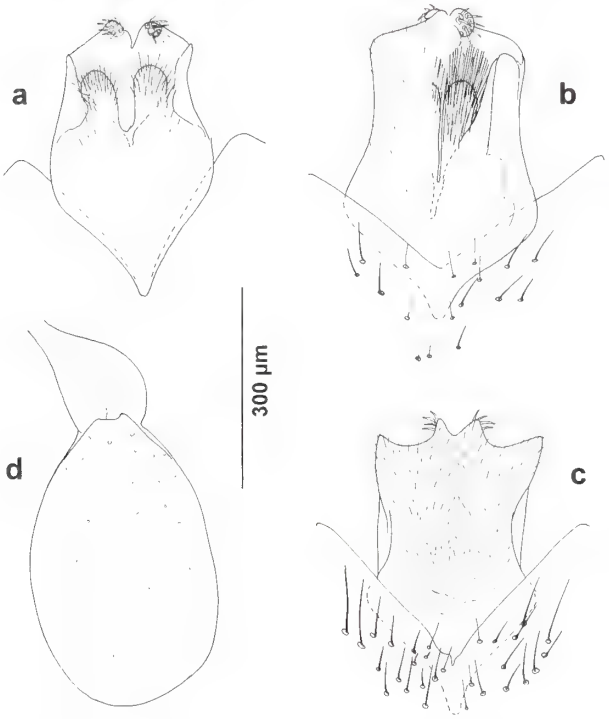

Fig. 4: *Bibiocephala* spp., oviscapts (a-c) and seminal receptacle (d), all to same scale. a, *B. grandis*, dorsal view of oviscapt; b, *B. infuscata*, combined ventral (left) and dorsal views (right) of oviscapt; c, d, *B. maxima*, ventral view of oviscapt and one of the two lateral receptacles.

Larvae (only last instar specimens with five to six gill filaments per tuft)

1 Six gill filaments per tuft; peristomal margin medially notched (labrum shorter than laterally adjacent areas; Fig. 2a); dorsal pseudopods slender and long, directed obliquely backward; ventral face laterally from suckers with heavy dark spine-like setae; dorsal face with flat sclerotized glossy calluses .... ***B. grandis*** Osten-Sacken

1' Five gill filaments per tuft; peristomal margin entire (Fig. 2b); dorsal pseudopods short, pointing sideways; ventral face laterally from suckers with short pilosity; dorsal face variable 2

2 Distinct sclerotized warts or calluses on dorsum; distal antennal segment little longer than basal one. Labrum with several long setae in addition to four normal setiform sensilla . ***B. infuscata*** (Matsumura) (*B. infuscata minor* Kitakami, 1931 is said to differ from *B. infuscata* by paler pigmentation and smaller size. *Bibiocephala jezoensis* (Matsumura), 1931, from Hokkaido was synonymized with *B. infuscata* (Zwick 1990). Largest species of genus).

2' No dorsal sclerotizations but sometimes low unsclerotized swellings present; labrum only with the normal four setiform sensilla; antenna variable 3

3 Distal antennal segment littler longer than basal one .... ***B. maxima*** Brodsky

3' Distal antennal segment almost twice as long as basal one .... ***B. komaensis*** (Kitakami)

4.1.2. *Bibiocephala maxima* Brodsky, 1954

(Figs. 1c, 3c, d, 4c, d, 5)

Bibiocephala maxima Brodsky, 1954 (Brodsky 1954: 229)

Our specimens from the entire known range match the description of *B. maxima* Brodsky, 1954 and we did not study types. Unfortunately, Brodsky (1954) compared *B. maxima* only with Nearctic *Bibiocephala*. *Bibiocephala maxima* occupies a vast range, from Kazakhstan and the Altai mountains to the Ayano-Mayski Region on the coast of the Sea of Okhotsk. Its southernmost Russian localities are not far from North Korea and Manchuria from where *B. komaensis* was recorded (see below). *Bibiocephala maxima* has clear to faintly tinged wings; despite its name it is smaller than *B. infuscata.*

Material (See Table 1; all in PZ). RFE03, 16 E; RFE06, 1♀, 49P, 6E; RFE08, Russian Far East, Primorje, Lazovka r. 25 km W of Lazo, at bridge, 13.06.1998: 1E; RFE09, 4E; RFE10, 2E; RFE14, 36P, 8E; RFE15, 3♂, 28P, 72E, 2L; RFE16, 4P, 2E; RFE21, 56♂, 3♀, 16 P, 31E; RFE27, 2♀; RFE28, 2♂, 1♀, 6E; RFE33, 2E; RFE35, 1♀, 1E; RFE38, 2E; RFE39, 2E; RFE40, 1♂; RFE41, 56♂, 3♀, 170P, 22E; RFE42, 8♂, 1♀; RFE47, 7♂, 14♀, 2P, 20E; RFE48, 2♂, 1♀, 6E; RFE49, 2P; RFE50, 48P, 2E, 1L4. Russian Far East: Ayano-Mayski Region, Aldoma R., 11/12.8.1999, M&T Tiunov, 2E. Khabarovsk Territory: Ochotsky Region, River Kuchtui, 10 km above mouth, 30.06.1999, 10.3°C, M.&T. Tiunov, 16♂, 1♀, 38P, 1L4.

Kazakhstan, surroundings of Ust Kamenogorsk [49°58'N, 82°36'E], V. Devyatkov (PZ): River Kurchum, 25.9.2002, 1 L3, 1L4; mouth of River Khamir (tributary of River Bukhtarma), 11.6.2003, 4♂, 1(♂).

Mongolia: Selenge, Khonin Nuga [49°05'260N, 107°17'440E], Eroo River, 21.VI.2003, P. Surenkhorloo, 1 pharate ♀, 8 pupal exuviae (PZ); Turgen-Gol [50°05'18"N, 91°37'50"E], 20.8.1997 and 17.8.1999, 8 L2, 22 L3, 4 L4, W. Horn & M. Paul, 27.8.1999 (SAWL); Tesiyn Gol [49°39'29"N, 95°43'47"E], W. Horn & M. Paul, 27.8.1999, 2 L3 (SAWL).

Larvae of *B. maxima* undergo considerable change during development. Second and 3rd instar specimens have six short dorsal spines on each abdominal segment, their arrangement is the same as the dorsal calluses in *B. infuscata*, or of spines in *Agathon* spp. Last instar larvae of *B. maxima* lack dorsal sclerotizations, but spatulate setae on the fore body become important. A few larvae collected in autumn looked very unfamiliar because they are freshly moulted, their gut still empty, and body not fully extended. In this condition, spatulate setae on head capsule and corners of prothorax stand close together and appear large, in comparison with the trunk; in places, the true body contour is veiled by setae (Figs. 5a, b). By spring, larvae accumulate much biomass whereby the body becomes extended, the head is pushed forward and downward; general shape is strikingly different from autumn specimens. Spatulate setae on fore body stand widely separate and appear tiny against extended body, remaining easily unnoticed. Figure 5c shows the single extended last instar larva not yet in prepupal condition that we have seen (Mongolian specimen); shape of its fore body resembles *B. infuscata*. In prepupae, corners of cephalic division are effaced, because of further body extension. Some Far Eastern last instar larvae look slightly variegated. They are light brown with anterior portions of several body divisions darker brown.

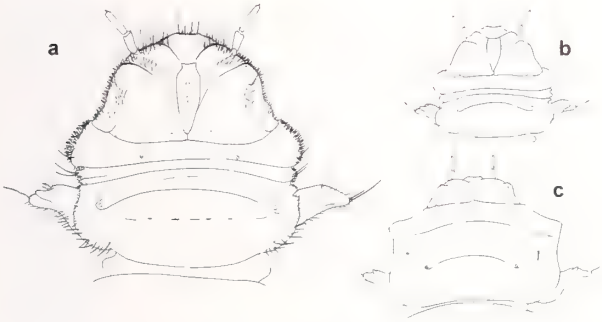

Fig. 5: *Bibiocephala maxima*, cephalic division of Mongolian last instar larvae. a, freshly moulted specimen showing arrangement of spatulate setae; b, same specimen, at same scale as specimen with extended fore body (c).

Biological notes. Larvae and pupae of *B. maxima* live on the underside of stones under which current rushes through and are never found on the upper side; the preferred larval habitat of *B. grandis* is similar (HOGUE 1982). *Bibiocephala maxima* emerges earlier than other net-winged midges in the Russian Far East. In early June, at several places, only fragments of pupal exuviae were left. Elsewhere there were many adults and pupae, but altogether only two prepupae were still found in June. The few earlier instars we saw were collected in autumn. Apparently the life cycle resembles *B. infuscata*, which hatches from eggs in autumn and overwinters in the 4th larval instar (KITAKAMI 1950). Hibernation of *B. maxima* larvae takes place under harsh environmental conditions. For example, winter temperatures are below -30°C near the Mongolian Turgen Gol, and a gauging station 25 km upstream from the sample site records no measurable discharge between December and March. The river bottom consists of coarse gravel with large near-surface interstitial spaces that may have contained flowing water also in winter (M. PAUL, pers. comm.).

HOGUE (1982) suggested that *B. grandis* might overwinter as eggs or very small larvae. However, the species probably has the same life cycle as the Asian congeners because large numbers of inactive, closely aggregated last instar larvae but no other life stage were collected immediately after snowmelt, in May, in the lower St. Vrain River, Colorado, and in several streams near Provo, Utah (P. Zwick). Indeed, 4th instar larvae were collected through the winter in Oregon, and even beneath winter ice in the Canadian Rockies (G.W. COURTNEY, pers. comm.).

Adult males resting in vegetation did not hang down from it like most other Blephariceridae. They often sat on grass stems, head up, grasping the support with all six legs. Because of the long hind legs, the body strongly diverged from the grass stem. Large swarms of only males were observed at Malinovka River with binoculars, in the morning and in the afternoon. Swarms were over land, 3-6 m above ground, above or on the sunny side of riparian willow bushes (*Salix* sp.). Specimens kept distances of 40-90 cm between each other, flying quietly in a floating manner. The front legs were held obliquely up and back between the wings, over the thorax, with the tarsal tips curved forward; short middle and very long hind legs hung down. Males that came close or other insects flying into the swarm, for example a fly (Calliphoridae), were rapidly approached from below by some swarm member and chased away.

At evening dusk, numerous males were noticed flying over swiftly and smoothly flowing sections of the upper Nemtu River. They flew upstream for short distances, then dropped back again. Various pale insects emerging from the river, mainly small Ephemeroptera and Plecoptera: Chloroperlidae were well visible under the low light conditions. Many of them suddenly changed direction of flight, or dropped abruptly. When caught with a net, the pale insect had each time been seized by a fully pigmented male *Bibiocephala*. In two cases, however, the pale specimen was a freshly emerged *Bibiocephala* female. It appears that males emerge before females and catch these for copula, upon evening emergence. Where and for how long females live is unknown. We saw only few females, either at emergence, or spent and dying between stones on the shore of River Khor, below Sukpai.

Distribution. *Bibiocephala maxima* was first described from the Altai. It occurs even further west, near Ust-Kamenogorsk. It is also widespread and common in the Russian Far East. The new Mongolian records fit in well. ZASYPKINA & RYABUKHIN (2001) report unidentified larvae of *Bibiocephala* from further northeast than the area sampled by us.

4.1.3. *Bibiocephala komaensis* (Kitakami, 1950)

Amika komaensis Kitakami, 1950 (Kitakami 1950: 41).

Material. *B. komaensis*: 1 last instar larva, Korea, Ryeongha, Hamgyeongbuk-do (= Reika, N. Korea), 12.6.1936, leg. Kawamura. In the same vial are also 1L2, 1L3, Hakugan, N. Korea, 6.9.1940, leg. Kitakami (ZFMK); all three specimens are syntypes. 1 specimen of each larval instar, syntypes (no locality data; USNM).

We were unable to borrow a larval syntype (Reika, N. Korea, leg. Kawamura 13.VI.1936) kept in Otsu Hydrobiological Station of Kyoto University (K. N. Satake 1988, pers. comm.). These few larvae seem to be all of the still remaining syntypes; we designate no lectotype.

In the very old material we cannot assess slight differences in body surface colour and gills between *B. infuscata* and *B. komaensis* which Kitakami mentioned. In the last instar, the long distal antennal segment distinguishes *B. komaensis* from *B. infuscata* (Kitakami 1950), and also from *B. maxima*. Details of the mouth region agree with *B. maxima*, and differ from *B. infuscata*. Pupal exuviae of *B. komaensis* agree with *B. maxima*, by Kitakami`s description; material is not available. Larval instars 2 and 3 lack dorsal spines, which are present in *B. maxima*; however, we saw few specimens.

Whether *B. komaensis* is really distinct from *B. maxima* cannot be decided in the absence of pupae and especially of adults of *B. komaensis*. The case of the two nominal species might resemble the species pairs *Agathon eoasiaticus* – *A. kawamurai, Philorus levanidovae* – *P. chosenensis,* and *Blepharicera parva* – *B. yamasakii*, see below.

4.2. Genus *Agathon* von Röder, 1890

Agathon von Röder, 1890. Type species: *Agathon elegantulus* von Röder, 1890: l.c.: 232 (von Röder 1890: 230).

Apomorphies supporting the monophyly of *Agathon* are found in the male genitalia: long widely separate male cerci connected only by a transverse basal bar (e.g., Fig. 6a). Mostly, cerci are slender straight rods although there is some variation in detail. For example, in *A. elegantulus* cerci are curved mediad and apically narrowed (see figures in Hogue 1973, 1987). In *A. setosus* sp. n. and *A. aylmeri* (Garrett, 1923) (Nearctic) their slightly enlarged apices are gently turned ventrad, etc. Vesica with transverse apodeme, not a vertical one, as normal.

Agathon was in the past confused with *Bibiocephala* because a remnant of wing vein R_2 is retained in some species; it lacks in others. However, aberrant specimens occur in either group; they have a remnant of R_2 in one wing only.

All Asian species are closely related and similar to the Nearctic type species. Outer dististyle bifid, shorter dorsal branch arises basally and may end before, or extend over, subapical modifications on dorsal face of ventral branch. In *A. elegantulus* and almost all other species a subterminal process or fold extends variably far across ventral branch so that a pocket or depression is formed between fold and apex proper (Figs. 7c, d, 9c, d, g). Inner dististyle very wide, a largely membraneous foliaceous structure (Figs 6a, 9h).

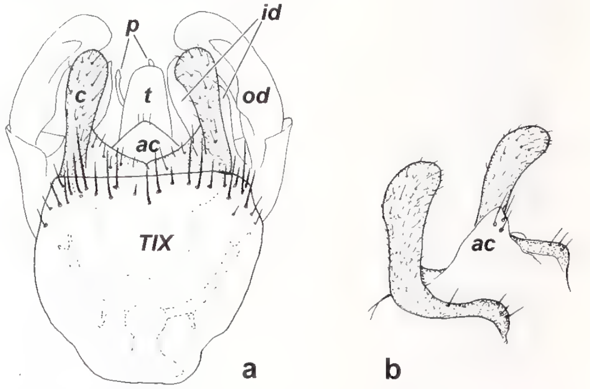

Fig. 6: *Agathon setosus* sp. n. a, male genitalia in dorsal view; b, cerci and anal cone in oblique posterior view from left side, to show connection of cerci to sclerites supporting anal pouch. ac, anal cone; c, cercus; TIX, tergite 9; p, paramere tips; t, tegmen; id, inner dististyle; od, outer dististyle.

The above diagnosis does not apply to *A. comstocki* (Kellogg, 1903) and *A. doanei* (Kellogg, 1900) whose relationship remains doubtful. The genus *Agathon* requires further study; its relations with *Asioreas* Brodsky in the Altai and Himalaya will be discussed separately (Zwick, in preparation).

Each lobe of the female oviscapt bears distally a broad spinuliferous dorsal callus (not narrow and finger-shaped like in *Bibiocephala*). Three spheroid to pyriform receptacles, basal half with tiny puncture-like pale spots, are sharply set off against short straight ducts. As usual, the median receptacle is more slender than the lateral ones.

We name a new species, raising the number of Russian species to four, all of which are found also in the Far East. The Russian species have closely similar relatives in Korea and Japan, respectively (Kitakami 1931, 1950) with which they were previously never compared. We have carefully compared these species and considered the Russian taxa are valid.

Several large samples contained also first instar larvae, which by their association with later instars, can preliminarily be assigned to *A. decorilarva* and *A. eoasiaticus*, respectively. We noticed no specific differences and none to distinguish them from first instar larvae of *Bibiocephala*.

4.2.1. Keys to *Agathon* species known or expected from the Russian Far East

Adult males (Keys to females not attempted)

1 Dististyle almost entire, dorsal lobe appears only as a subapical tooth (Fig. 6a) .... ***A. setosus*** sp. n.
1' Dististyle deeply divided into dorsal and ventral lobes, ventral one longer 2
2 Dorsal lobe extends to or over subterminal tooth or crest on ventral lobe of slender dististyle 3
2' Dorsal lobe of dististyle short, strong transverse crest across ventral lobe exposed. Ventral lobe apically very wide, transversely truncate (Fig. 9g) .... ***A. ezoensis*** (Kitakami)
3 Ventral lobe of dististyle dorsally with subapical tooth (Fig. 7c) .... ***A. decorilarva*** Brodsky
3' A subapical crest extends across dorsal face of ventral lobe of dististyle (Fig. 9c) .... ***A. eoasiaticus*** Brodsky, ***A. kawamurai*** (Kitakami)

Pupae

1 Outer respiratory lamellae rounded with narrow base (racket-shaped), respiratory organs prostrate (Figs. 11a-c) .... ***A. setosus*** sp. n.
1' Respiratory organs erect, lamellae slender, tongue-shaped 2
2 Anterior end of pupa in dorsal view regularly truncate to rounded, cephalic sclerite not recessed between lateral lobes of pronotum .... ***A. decorilarva*** Brodsky
2' Anterior end of pupa in dorsal view with cephalic sclerite recessed between anteriorly projecting lateral lobes of pronotum .... ***A. eoasiaticus*** Brodsky, ***A. ezoensis*** (Kitakami), ***A. kawamurai*** (Kitakami)

Larvae (final instar)

1 No spines or pointed granules on dorsum, only long soft setae on sides of body present (Fig. 8d) .... ***A. setosus*** sp. n.
1' Larval dorsum with pointed granules or long spines 2
2 Six long erect spines on each abdominal segment (Fig. 8a) .... ***A. decorilarva*** Brodsky
2' Dorsal armature consists of pointed granules not or hardly higher than width at base, and/or transverse rows of erect spinules 3
3 Six well developed granules or short spines per abdominal segment (Fig. 8b); no rows of spinules. Thorax with single short spinule row immediately behind cephalic sclerites. Dorsal pseudopods with blunt dorsal knee .... ***A. eoasiaticus*** Brodsky
3' Abdominal segments with two spinule rows, among which dorsal warts may or may not be distinct (Fig. 8c). Thorax with more spinule rows 4
4 Three thoracic spinule rows (N. Korea) .... ***A. kawamurai*** (Kitakami)
4' Two thoracic spinule rows (Hokkaido, Sakhalin, Iturup I.) .... ***A. ezoensis*** (Kitakami)

4.2.2. *Agathon decorilarva* (Brodsky, 1954) (Figs. 7, 8a)

Bibiocephala decorilarva Brodsky, 1954 (Brodsky 1954: 236).

Material. *Agathon decorilarva* was described from syntypes from: "Altaj: r. Yan-Tsili; r. Korbu; r. Kokschi; r. Bolschoj Korbu; r. Abakan; S. Primorje: r. Sitsa; Pigarejeva gorge in St. Tigrovaja; Sutsan, r. Kamen; r. Kuatru, Kuretski Mts". We studied some larval syntypes (ZIAS) labelled: *Bibiocephala decorilarva* sp. n. det. K. Brodskii // [illegible abbreviation] 64 [illegible abbreviation] 78.

The species is common and widespread in rhithral streams in the Russian Far East, see also Zasypkina & Ryabukhin (2001). Material from localities in Table 1 (all in PZ): RFE04, 1P; RFE06, 7P, 7L4; RFE07, 57P, 11L4; RFE08, 21P, 2L4; RFE09, 1P; RFE12, 6E, 23L4, 28L3; RFE13, 55L4; RFE14, 17P, 22L4, 1L3; RFE15, 17P, 23L4, 1L3; RFE16, 1L4; RFE17, 2♂, 1♀, 131P, 59E, 8L4 ; RFE18, 8P; RFE19, 50P; RFE20, 41P, 10E, 2L4; RFE21, 60P, 1L4; RFE22, 1♂, 10P, 10L4; RFE25, 1♂, 1P, 14L4; RFE26, 6P, 5E, 1L4; RFE27, 1♂, 50P, 6E, 23L4; RFE28, 3♂, 1♀; RFE28, 52P, 18E, 1L4; RFE33, 18P, 4E, 1L4; RFE34, 1P; RFE36, 16P, 10L4, 1L3; RFE37, 21P, 3E, 2L4; RFE38, 1P; RFE41, 4♂, 80P, 65L4; RFE42, ca. 20P, 4L4; RFE43, 1P, 5L4; RFE44, 64L4; RFE45, 1L4, 11L3, 118L2, 1L1; RFE46, 41L4, 24L3; RFE49, 18P, 52L4, 10L3; RFE49a, 10L4, 5L3; RFE50, 2P, 8L4, 2L3.

Additional material from the Russian Far East (PZ): Amur River Basin, I.M. Levanidova: Ali River, 23.07.1959, 10L, 8P; Iski River, 02.07.1961, 4L. Magadan Territory, Makarchenko: Dukcha River, 7, 9.7.1979, 99L; 23.07.1979, 8L; Motyklejka River [Motyklejka 59°34'N, 148°38'E], 13,14.7.1977, 17L; Ulakan River, 17.07.1977, 6P, 2L. Ayano-Mayski Region [Ayan 56°27'N, 138°10'E], M&T Tiunov: Uika River 1 km upstream of mouth, 21.-26.7.1999, 11L4, 14-15.8.1999, 9P; Ulujkan River, Lantar River basin, 29.07.1999, 19P, 8L4, 1L3; Aldoma River, 11/12.8.1999, 12♂, 8♀, 22P; Lantar River, 2.5 km upstream from mouth, 28.07.1999, 2♂, 1♀, 28P, 2L4.

Kamchatka, I.M. Levanidova (PZ): Kirpichnaya River, 18.7.1968, 11P, 4E; River Ewpitwajam (Lake Palanskoje), 18.8.1963, 6P, 9E; nameless stream near village Zhupanova, 20.07.1964, 1L; Talalayevka River, 04.08.1972, Nikolayeva, 1L.

Descriptive notes. Brodsky (1954) described all stages and both sexes. He compared *A. decorilarva* with three Japanese species, *A. japonicus* (Alexander, 1922), *A. montana* (Kitakami, 1931), and *A. bispina* (Kitakami, 1931), none of which is really similar. We establish distinctness of *A. decorilarva* from several much more similar Japanese species that were not considered by BRODSKY (1954).

Adult. R_2 present. Spur formula 0.0.2 in both sexes. Spurs on hind tibia very unequal in size.

Male (Figs. 7a, c, d): Eyes widely separate, upper section little developed. Rostrum shorter than head height. Antenna short, with 14 segments, terminal one not longer than penultimate and only slightly constricted. Genitalia slender, outer dististyle with narrow apex and incurved tip; subterminal fold short, almost tooth-like. Dorsal branch of dististyle curved, extends to close to subterminal fold.

Female (Figs. 7b, e): Eyes large, narrowly separate, upper section fully developed. Antenna even shorter than in male, barely reaching tip of rostrum. Rostrum only as long as head height but fully developed. Oviscapt with slightly concave sides and tongue-shaped distal lobes; spermathecae subspherical to ovoid.

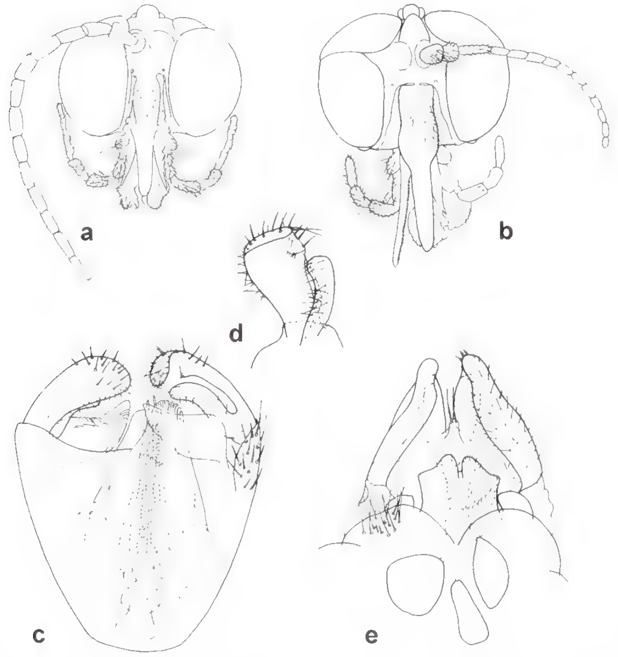

Fig. 7: *Agathon decorilarva*. a, b, head of pharate male and female , respectively; c, male hypopygium (tergite 9 and cerci removed); d, oblique dorsal view of left outer dististyle; e, female terminalia. Not to scale.

Pupa. Typical of genus, zig-zag pattern across thorax. Very similar to *A. eoasiaticus* (see BRODSKY 1954: figs. 4/6+7), respiratory lamellae less than twice as long as wide at base, lamellae set in an oblique row so that opposite first lamellae are wide apart while lamellae 4 are closer together, their slightly recurved tips meet, or almost so. Bases of lamellae on the outside terminating in integument as simple straight lines. The endpoints of the four lamellae lie on a slightly convex line because lamellae 2 and 3 project slightly further sideways than lamellae 1 and 2. Cephalic sclerite not distinctly recessed between fore leg sheaths.

Larva. Long erect spines, anterior ones longer and closer together than posterior ones (Fig. 8a). Lateral ones on segment seven smaller, about half the length of dorsal ones. Integument very variably contrastingly patterned, from mainly yellow to mainly dark. Also spines (all or only some) dark or yellow. Head capsule variably patterned in yellow and dark, often an extended pale center near anterior end of median frontal sclerite, lateral frontal sclerites with distinct yellow eye-brow-like mark above oblique suture. However, head capsule may also be almost completely black. Ventral pseudopods slender, with narrow recurved apex, posterior margin distinctly concave. Dorsal pseudopods slender, with erect narrow pointed subterminal outgrowth on narrow tip of pseudopod.

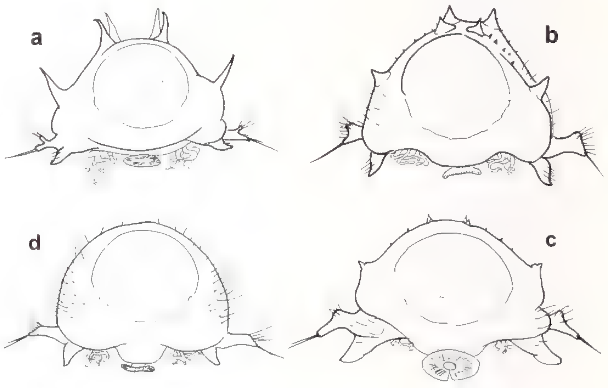

Fig. 8: *Agathon* ssp., cross-sections through larvae, 3rd abdominal segment from behind, diagrammatic. a, *A. decorilarva*; b, *A. eoasiaticus*; c, *A. ezoensis*; d, *A. setosus*. Not to scale.

Comparisons. *Agathon decorilarva* is a close relative of (but certainly distinct from) two Japanese species whose larvae also have long erect spines and sharply angled dorsal pseudopods. *Agathon bilobatoides* (Kitakami, 1931) has only the four central spines large. It also possesses additional transverse rows of abdominal thornlets, also three rows on the thorax. The subterminal fold on the male dististyle is long, standing in an oblique position. The pupal gill lamellae are closely packed, all semicircularly curved towards middle, with tips of opposite organs meeting. *Agathon longispinus* (Kitakami, 1931) has the median spines on the larval abdominal segments 2 and 3 connected by a transverse bar-like socket, and lateral spines on segment 7 are tiny, much shorter than on the other segments. Pupal lamellae more slender than in *A. decorilarva* (>3 times longer than wide at base), divergent, from 1st to 4th successively more curved and directed medially, tips of 4th lamellae meeting. Male with long antenna (reminding one of *A. eoasiaticus*), dorsal branch of male dististyle short, with strongly widened apex.

In the Russian Far East, *A. decorilarva* and *A. eoasiaticus* often coexist; pupae can be distinguished by the relative length of the cephalic sclerite versus leg sheaths. This character can no longer be assessed in pupal exuviae which can, however, be identified by the shape and position of the outer endpoints of the four respiratory lamellae.

4.2.3. *Agathon eoasiaticus* (Brodsky, 1954)
(Figs. 2c, 8b, 9)

Bibiocephala eoasiatica Brodsky, 1954 (Brodsky 1954: 234).

Material. We identified the species from the description and saw no types. We did not find the species at the type locality ("St. Tigrovaja, tributary of r. Sitsa; Pigarejeva gorge") but Stations RFE01 and RFE03 are close to it: RFE01, 11.06.1998, 330L4, 25L3; 26.06.1998, 3 ♂, 322P, 15E, 79L4, 12L3; RFE09, 1L4, 1L3; RFE10a, 7P, 5E; RFE12, 1L4, 2L3; RFE15, 1♂, 3♀, 1P, 4E; RFE19, 3P, 3E; RFE20, 4P, 1E; RFE21, 1L2; RFE22, 3♂, 2♀, 225P, 9E, 20L4; RFE24, 1♀, 1P, 2E; RFE25, 2♀, 2E; RFE27, 3♀, 1P, 2E; RFE28, 1P; RFE31, 10♂, 3♀, 129P, 14E, 8L4; RFE33, 1♀, 1P, 3E; RFE34, 4♂, 1♀, 134P, 20E, 5L4; RFE36, 28P, 23E; RFE37, 6P, 12E, 1L2, 1L1; RFE41, 5♂, 3♀, 2P, 94P, 7E, 22L4; RFE42, 22P, 5L4; RFE44, 38L4; RFE49, 92P, 27L4; RFE49a, 1P, 15L4; RFE54, 12P, 8E; RFE55, 9♀,1E, 1L4 (all in PZ).

Mongolia, Selenge, Mandal, leg. P. Surenkhorloo (PZ): Khonin Nuga [49°05'260N, 107°17'440E], Tsagaan Chubut River, 30.VI.2003, numerous L3, L4, 8 P. Bar-Chuluut River [48°58'638N, 106°57'013E], 13.VII.2003, 6P (incl. 3♂). Bar-Chuluut River [48°58'368N, 106°59'564E], 4.VIII.2003, 2♂, 2♀. Eroo River near confluence with small tributary [49°05'260N, 107°17'440E], 01.VII.2003, 2 L4. Ataa River, 18.VII.2003, 56P (incl. pharate ♂♂), 3Ex, 3L4, 1L3 (all in PZ).

Adult. Previously unknown. R_2 present. Spur formula 0.2.2 (females) and 0.0.2 (males). Spurs on hind tibia unequal in size, those on female middle leg minute, not easily seen.

Male (Figs. 9a, c, d): Antenna more than twice as long as head with rostrum, individual flagellar segments long, last one strongly bottle shaped. Genitalia compact, hypopygium rounded. Distal edge of dorsal dististyle wider than in *A. decorilarva*, truncate, prominent subterminal fold across ¾ of dististyle width. Fold hidden by longer, slightly club-shaped dorsal branch of dististyle.

Female (Figs. 9b, e): Very similar to *A. decorilarva*, rostrum and antenna slightly longer. Oviscapt appears slightly more elongate but is not distinctive. Receptacles subspherical to ovoid.

Pupa. Resembles *A. decorilarva*, but cephalic sclerite distinctly recessed between leg sheaths. Bases of lamellae terminating in integument as simple straight lines. On outside, endpoints of lamellae 2-4 lie in straight line while lamella 1 projects distinctly further sideways and ends in small backwardly turned hook.

Larva. Short brown or yellow spines on pale sockets (Fig. 8b), or only distinct cones on abdominal segments, sometimes two or three small cones together instead of spine. Anterior spines or cones higher and more widely apart than posterior ones. Integument greyish, not contrastingly patterned. Head capsule with pale center near lower end of median frontal sclerite, remainder amber to dark brown; oblique suture across lateral frontal sclerites sometimes apparent as pale narrow line. Thornlets in transverse rows, tiny, but of variable expression; all abdominal and three thoracic rows may be present. Dorsal pseudopod plump, with obtuse rectangular knee instead of a dorsal process.

Comparisons. *Agathon eoasiaticus*, the Korean *A. kawamurai* (Kitakami, 1950), and the Japanese *A. ezoensis* (Kitakami, 1950) and *A. bispinus* (Kitakami, 1931) are similar. The last is from Honshu and not available to us; only larvae and pupae were described.

Male genitalia of *A. ezoensis* are distinct (see below) but those of *A. kawamurai* are not. Females (all with large upper portions of eyes, with large reddish ommatidia) and pupae are so similar that in view of the limited material available of the Japanese and Korean species, we attempt no distinction.

Larvae can be distinguished by the dorsal armature of thornlets and spiny warts. Kitakami (1950) used presence/absence and number of transverse rows of thornlets on thoracic and abdominal segments and the relative size of six dorsal warts to distinguish the taxa. In *A. eoasiaticus,* the six dorsal warts are all larger than the thornlets, the anteromedian pair being largest. In the other species (Fig. 8c; *A. ezoensis*), at best the lateral warts are distinct while the dorsal ones are effaced and barely larger than spinules in the transverse rows. However, *A. eoasiaticus* varies, both within and between samples. There may be 0-3 rows of thornlets on the thorax, and none, indistinct, or two distinct rows on the abdomen. The main warts may be prominent and stand by themselves, or be less distinct from adjacent thornlets. Warts may have several points each, or essentially consist of a closely set group of thornlets. The distinction of larvae remains therefore provisional until more material of the relatives of *A. eoasiaticus* becomes available.

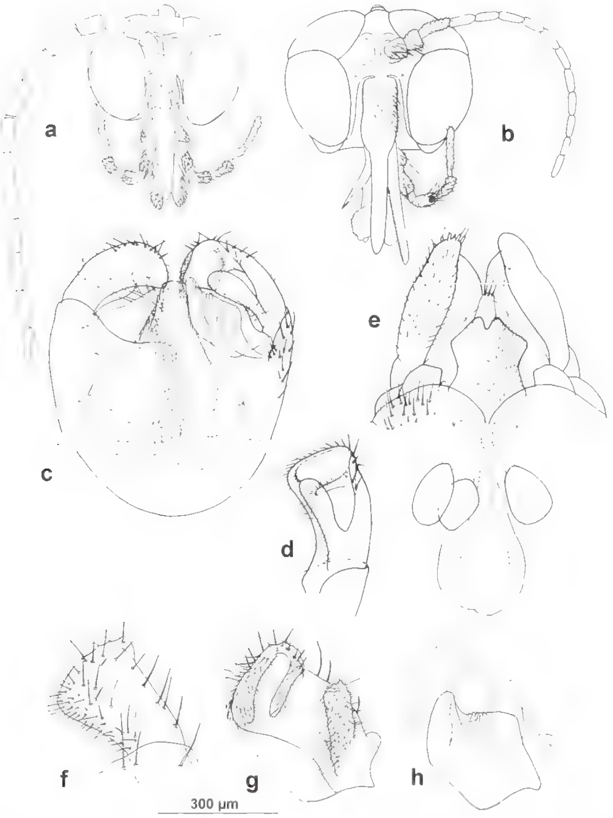

Fig. 9: *Agathon eoasiaticus*. a, b, head of pharate male and female, respectively; c, male hypopygium (tergite 9 and cerci removed); d, dorsal view of left outer dististyle; e, female terminalia. *A. ezoensis*. f, g, left outer dististyle in ventral and dorsal views; h, same as g, inner dististyle added. Not to scale.

4.2.4. *Agathon kawamurai* (Kitakami, 1950)

Bibiocephala kawamurai kawamurai Kitakami, 1950 (KITAKAMI 1950: 44).

Material. *Bibiocephala kawamurai kawamurai* Kit., 1♂ (lectotype, here designated), 1♀, 2P (genitalia of pharate ♂ on slide), 2L4 (paralectotypes, here designated), Korea, Baekam, Hamgyeongbuk-do (= "N. Korea, Hakugan"), 23.VII.1939 (ZFMK); additional paralectotypes; 1♂, 1♀, 2P, 2L4 (one lacking cephalic division) (USNM).

Taxonomy. KITAKAMI (1950) suggested "perhaps we can expect this species in Manchuria". Male genitalia do not differ from *A. eoasiaticus*. The nominal taxa may nevertheless be distinct because the rostrum of *A. kawamurai* attains not even head height. *Agathon eoasiaticus* (Fig. 9a) has also longer antennae than *A. kawamurai*. Larvae of *A. kawamurai* have the full set of transverse rows of prominent thornlets among which dorsal warts are indistinct. However, larval armature of *A. eoasiaticus* is variable. The variation of the widespread *A. eoasiaticus* may eventually be found to encompass the structural variants presently distinguished as *A. kawamurai*, which would become the valid name.

Comments. KITAKAMI (1950) made no distinction between specimens known to him, which therefore are all equal syntypes. Consequently, the specimens in USNM must have type status, even though their precise collection data are unknown. We have not seen syntypes from Ryeongha, Hamgyeongbuk-do (= Reika) in North Korea in Otsu Hydrobiological Station: 2L3, 2L2, 12.VI.1936 (Kawamura) and 1♂, 1♀, 2P, 2L4, 22.VII.1939 (Kitakami).

4.2.5. *Agathon ezoensis* (Kitakami, 1950) (Figs. 9f-h)

Bibiocephala kawamurai ezoensis Kitakami, 1950 (KITAKAMI 1950: 46).

Material. *Bibiocephala kawamurai ezoensis* Kit., 1♂ (lectotype, here designated) 2P (paralectotypes) [Takinozawa, S. Saghalien, 20.VII.1936]; 2L4 (paralectotypes) [Sôunkyo, Hokkaido, 25.VII.1936] (ZFMK). Additional paralectotypes without locality data: 1♂, 1P, 2L4 (USNM).

Additional material (PZ): Kuriles, Southeastern Iturup Isl.: Usach waterfall, 29.07.1998, T. Arefina & V. Teslenko, 1♀, 10P, 6L4, 1L3; unnamed stream with waterfall nr Usach waterfall, 29.7.1998, T. Arefina, 4♂, 1♀, 3P.

Very similar to *A. eoasiaticus* but R_2 normally absent. However one of the males in USNM and also one from Iturup Island have a remnant of R_2 in one wing.

Male genitalia (Figs. 9f-h) distinguished by outer dististyles with very wide apex and a short dorsal branch not closely appressed to larger ventral branch. Subterminal transverse fold across ventral branch of dististyle long, prominent, and exposed. Its caudal edge curves mediad and connects to apical edge, the curved connection projecting distinctly beyond general contour of dististyle. Inner dististyle wide, medial part distinctly elongated and projecting.

Presently females not separable from *A. eoasiaticus* by external characters because lack of R_2 in *A. ezoensis* is no reliable difference. Receptacles not examined. For pupae and larvae (Fig. 8c), see under *A. eoasiaticus*.

Remarks. Like *A. kawamurai*, this taxon was named from many syntypes from several localities in Hokkaido and on Sakhalin, between which no distinction was made in the description; therefore, the specimens in USNM are syntypes even though locality data are missing. The locality information for the specimens in ZFMK (in square brackets) is from the list that accompanies KITAKAMI'S material in coll. MANNHEIMS.

4.2.6. *Agathon setosus* sp. n. (Figs. 6, 10, 11)

Material. Russian Far East: Holotype (pharate ♂), paratypes (6 pharate ♂, 2 pharate ♀, 9P), [2773] Primorje, Sikhote-Alin, Edinka River, 10.08.1979, leg. Timoshkin. (Presently in PZ, will eventually be deposited in a museum).

Additional material: Primorje, Sikhote-Alin, Ada River, Bikin River basin, 22.07.1979, 4L, leg. Timoshkin. – Magadanskaya obl., Talok Stream at Susuman Town, Kolyma River basin, leg. Samokhvalov, 10.4.1982, 17 L; Khabarovskii krai, Basilii Stream, Tumnin River basin, 16.7.1997, leg. Tiunov, 1L. Mongolia, Selenge, [49°05'260N, 107°17'440E], Eroo River near confluence with small tributary, 01.VII.2003, P. Surenkhorloo, 5P, 8L4 (including prepupae) (all in PZ).

Adult. Adults apparently similar to previous species in size, venation, and colour; details unknown because only pharate specimens are available. Spur formula 0.0.1 in both sexes, both with small, widely separate eyes (Figs. 10a, b). Upper eye portion distinct but only small part of total eye area and not larger-facetted than lower part. Female with, male without functional mandibles and serrate hypopharynx. Antenna and palpus slender, much like *A. eoasiaticus*.

Male genitalia (Fig. 10c): Widely separate, long and slender cercus (Fig. 6) distally slightly enlarged and gently curved ventrad. Outer dististyle slender and narrow, with faint mediobasal swelling. Dorsal branch fused to ventral one over most of length, free tip resembles subapical tooth on ventral branch. Apex of ventral branch appearing simple because transverse fold practically apical, vertical fold separating it from ventral face visible only in apical view. Inner dististyle slender, more sclerotized and narrower than in relatives.

Female genitalia (Fig. 10d) similar to other species, oviscapt appears shorter and stouter. Seminal receptacles distinctly pyriform.

Pupa (Fig. 11). General shape normal except respiratory organs prostrate, less raised than in majority of species, extending distinctly further forward than long sheaths of fore legs which include wide straight front margin of cephalic sclerite between them. Outer lamellae racket-shaped, base narrower than distal part, stiff and shiny, distinctly wider than soft medial lamellae. Mesonotum with strong zig-zag folds. Dorsal granulation of metathorax and abdomen strong in middle, increasingly finer towards sides, lateral granules only 1/4 size of middorsal ones.

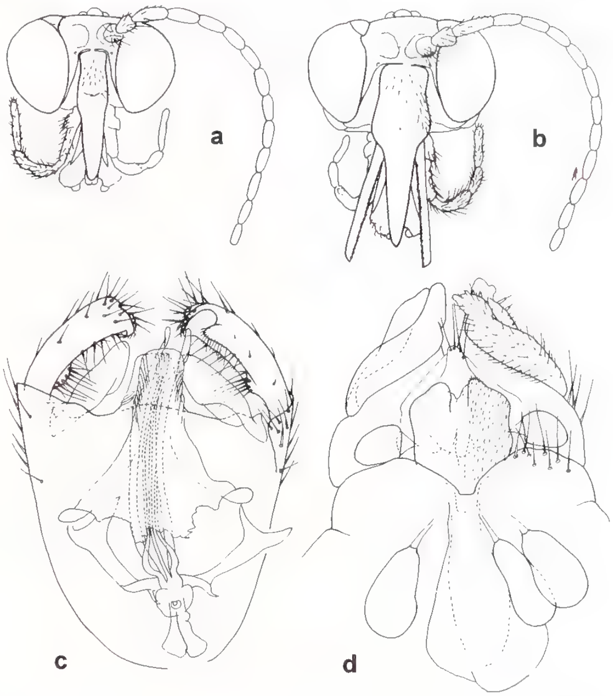

Fig. 10: *Agathon setosus* sp. n. a, b, head of pharate male and female respectively; c, male hypopygium (tergite 9 and cerci removed); d, female terminalia. Not to scale.

Larva. General shape resembles relatives. Cephalic sclerites amber, triangle above mandibles black, brown seams along anterior tentorial invaginations and along outer edges of medial and lateral frontal sclerites. Medial frontal sclerites additionally with faint traces of two usual brown longitudinal lines. Antenna 3-segmented. Body naked except long flexible setae arising from distinct insertion points, mainly on posterior segment halves. Ventral pseudopods simple, dorsal ones almost simple, only faint angle in dorsal contour (Fig. 8d).

Comparisons. The male genitalia are exceptional because the dorsal branch of the dististyle is not a freely projecting finger. Apex of outer dististyle and relatively narrow inner dististyle also unique. Pupa distinctive through its prostrate respiratory organs with stiff rounded outer lamellae much wider than median ones. Larva unusual in having long slender erect fine setae, instead of the usual cones, spines or stout thornlets. At first glance, larva appears naked and insofar resembles *A. montanus* (Kitakami, 1931) from Japan which, however, has prominently angled pseudopods. In particular, its exposed pseudopod 7 is so positioned that it resembles a backwardly bent knee. In contrast, pseudopods of A. setosus are almost simple.

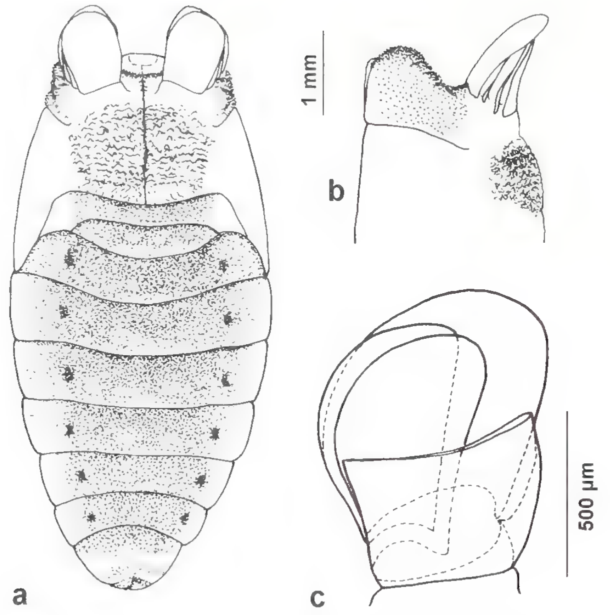

Fig. 11: *Agathon setosus* sp. n. a, pupa in dorsal view; b, front end seen from left side; c, left respiratory organ, lamella 4 partly cut to expose lamellae two and 3. Figures a and b to same scale.

4.3. Genus *Philorus* Kellogg, 1903

Philorus Kellogg, 1903 (Kellogg 1903: 199). Type species: *Blepharocera yosemite* (Osten-Sacken, 1877), by subsequent designation of Coquillett, 1910 (Coquillett 1910: 588).

The phylogenetic relations of *Philorus* among Blephariceriini are doubtful because the genus still shares presumably primitive characters with *Bibiocephala* and *Agathon*; see under *Bibiocephala.* At the same time, the radial vein is more reduced (two short branches on a long stalk, instead of long independent branches) than in other Blephariceriini, supporting monophyly of genus *Philorus*. The pupal respiratory organ of four low, widely divergent lamellae is another obvious apomorphy.

The genus comprises almost 25 species from mainland Asia (south to Assam and west to Tian Shan), Japan, and western North America. Grouping of included species is not yet generally clear. However, the new Russian species clearly belongs to a monophyletic group distinguished by: lateral digitiform appendages on male tergite 9; male with extremely short ventral bridge from which the bag-like, uncrested vesica extends freely forward; pupal respiratory organs medially touching, lamellae very low, crest-like, divergent.

The name *Euliponeura* Tonnoir, 1930 would be available for this group which comprises *P. asiaticus* Brodsky, 1972, *P. assamensis* (Tonnoir, 1930), *P. chosenensis* Kitakami, 1931, *P. horai* (Tonnoir, 1930), *P. longirostris* Kitakami, 1931, *P. minor* Kitakami, 1931; not all of the three characters listed above are known for each included species. Recognising *Euliponeura* would turn the genus *Philorus* paraphyletic because the last two apomorphic characters in the above list are shared by *P. vividis* Kitakami, 1931 (Zwick, 1997a). A complete phylogenetic analysis of the genus must be performed before any formal change of taxonomic status of included groups.

4.3.1. *Philorus levanidovae* sp. n. (Figs. 12, 13)

Material: Holotype pharate ♂, paratypes 1 pharate ♂, 2 pharate ♀, 4♂, 8♀ plus 4L1, 18L2, 35L3, 16P, 3E (some on slides) without type status: Russian Far East, Khasanski Region, Gryaznaya stream, Kravtsovski Cascades, 12. and 17.07.1998, T. Tiunova and T. Arefina (presently in PZ).

Additional material: Russian Far East, Primorje, small tributary to Vodopadnaja River at forest edge nr Nikolayevka, E of Partizansk, 12.06.1998, 5L1, 13L2, 8L3, 20L4 (PZ).

Adult. General structure, especially wing venation, typical of genus. Small, wing length: ♂ 5.5 mm, ♀ 7.5 mm. Pale, dorsal aspect of head, thorax and abdomen light brown, antennal flagellum and male genitalia brown, remainder yellowish.

Eyes widely separate, a tiny elongate-oval portion of eye towards ocelli more reddish, more finely facetted than the rest from which it is not set off by line of separation. Ocelli on flat wide frons, not raised on turret. Antenna with 13 segments, the 11 flagellar segments elongate and asymmetrical: dorsal contour straight with short seta at base, ventral side with distinct basoventral swelling.

Several structures sexually dimorphic. Antenna: each segment about 2.8-3.2 times as long as maximum width in males, 2.6-2.8 times in females (pharate specimens). Last segment 3.7x longer than wide in males, but similar to other segments in females. Mouthparts: rostrum of male shorter than height of head, no mandibles, no serrate hypopharynx. Palpus of ♂ short, segment four with prominent subterminal swelling, segment five long, whip-like, bare except some setae on convex face. Female rostrum slightly longer than height of head, with serrate hypopharynx and mandibles, mandibles longer than labrum. Palpus of ♀ generally similar to male but much longer. Scattered lateral setae along base of labrum in female, male without. Legs long and slender, unmodified. Tibial spurs hairy, spur formula 0.0.1 in males, 0.0.2 in females, spurs on hind tibia very unequal.

Male genitalia (Figs. 12a, b): Epandrium transverse, broad, setose, particularly strong setae bordering concave rear edge. Cercus simple, conical, setose, proctiger with two setae projecting below. Hypopygium transverse and short, distal margin in middle slightly triangular. On either side of dorsal face of gonocoxite arises sclerotized erect finger with strong apico-medial setation. Outer dististyle profoundly bilobed. Dorsal branch with blunt setose medial projection at base, apex of branch slender, bent anteromediad, with strong apical spines. Ventral branch largely soft, surface covered with microtrichia, rough. From an apical oval lobe with few large ventral setae hangs dorsally flat but ventrally keeled appendage. Band-shaped medial edge of appendage with microtrichia, semicircular lateral portion with hyaline outwardly directed spicules. Inner dististyle slender in form of dorsally hooked rod. Tegmen not apparent. Inner sclerites: ventral bridge shallow, vesica in form of oval sac without apodeme; three subequal penis filaments. Parameres longer and wider than penis filaments, apically widened, canal distinct, with funnel-shaped apical opening.

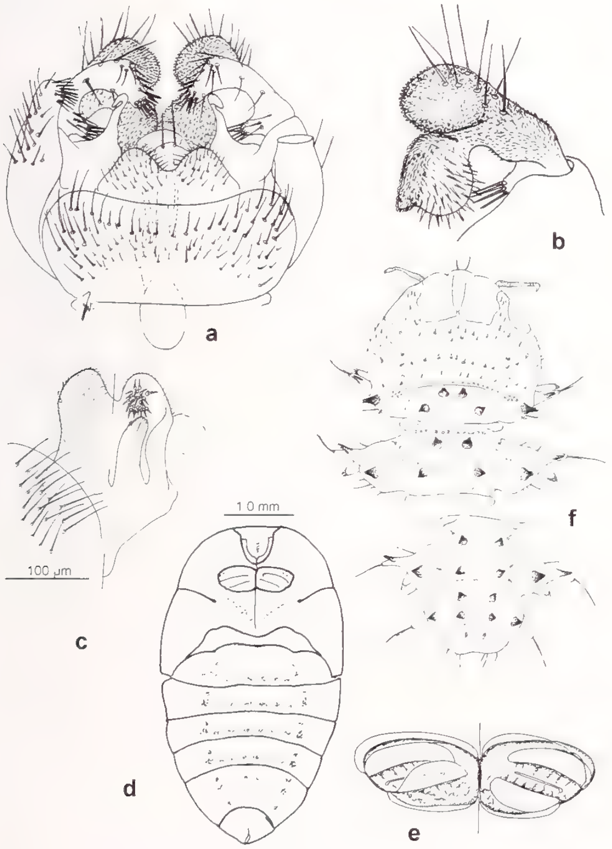

Fig. 12: *Philorus levanidovae* sp. n. a, male genitalia, dorsal view, left finger-shaped process cut; b, right dististyle, ventral view; c, female oviscapt; ventral view to the left, dorsal view to the right of the interrupted vertical line; the single curved spine on the side of one oviscapt lobe is apparently abnormal; d, pupa, dorsal view; e, pupal respiratory organs, dorsal view; slide preparation, position of lamellae caused by pressure of cover slip; f, last instar larvae, anterior and posterior body portions, dorsal views.

Female genitalia (Fig. 12c): Sternite 9 forms two semicircular lateral lobes with long setation including tongue-shaped base of oviscapt between them. Oviscapt plump, lobes rounded, separated by U-shaped notch. Microtrichia on ventral oviscapt face arranged in regular curved lines, middle strip bare. Dorsal face of each oviscapt lobe with about 15 grouped stout short curved setae just beyond apex of tongue-shaped process originating at oviscapt base; apex of process with slender microtrichia. Three pyriform spermathecae with short simple ducts.

Pupa. 4.7-6.5 mm long, flat. Pale brown. Granulation exceedingly fine and pale. Contour ovoid, front blunt, little wider than rear (Fig. 12d). Respiratory organs meeting medially, lamellae reduced to shallow crests. Outer lamellae form a low transparent rim around rough and partly wrinkled respiratory field. Slightly higher soft central lamellae 2 and 3 differ in length and distance from margin (Fig. 12e). Straight, open spiracular slit separating central lamellae; outer end of slit terminating in visible spiracular pore.

Larva. Last instar up to 7.5 mm long (Fig. 12f). Cephalic sclerites distinctly divided. Antenna about as long as cephalic sclerites, with long pale median zone. Antenna 2-segmented, separated by long ill-defined articular membrane. Sometimes, dark basal segment with narrow pale zone in middle, antenna then seemingly 3-segmented. Thoracic segmentation indistinct because segmental transverse rows of little erect spines on cephalic body division are irregular and somewhat obscured by numerous additional spinules. Abdominal tergites 1-6 with six pointed cones, each with several small spines at top. Two paramedian cones anteriorly, the other four widely spaced in posterior transverse line. Additionally, a pointed projection on elongate dorsal feeler situated above simple pseudopod. Segment 7 lacking pseudopod as well as cone on dorsal feeler. Remnant of tergite 8 with two small raised warts. Posterior margin of anal body division shallowly bilobed. Ventral face typical, six suckers, six pairs of gill tufts, five filaments in each; four rectal papillae surrounding last sucker from behind. Gills are so positioned that they are not normally visible in dorsal view. Lobes of rear body edge with shiny medially divided sclerite band. Instars 3 and 2 similar, with three and one gill filament per tuft, respectively. Cephalic sclerites in instars 1-3 with distinct posterior growth zones.

First instar larva (Fig. 13). No gills; rectal papillae present. Elongate egg burster on median frontal sclerite. Body surface finely wrinkled and with tiny flat cuticular spikes arranged in transverse slightly raised lines, crest-like. Long crest on only two of three thoracic segments and on abdominal segments 1-7. This long crest also includes pair of tiny cone-shaped and minute hairlike sensilla (tergal and subtergal sensilla, HOGUE 1978). Laterally, crest ends on small hump with 2-3 stronger spines above pseudopod (probably tergopleural sensilla of HOGUE 1978). Abdominal segments 1-7 additionally with short anterior crest lacking sensilla. Rudimentary segments 8 and following without crests and sensilla. Base of pseudopod with two, rarely three spines and tiny hair sensillum. Distally, each pseudopod with single very long seta and about 12 transparent rearward directed slender spines. Length of spines in each group increases from front to rear.

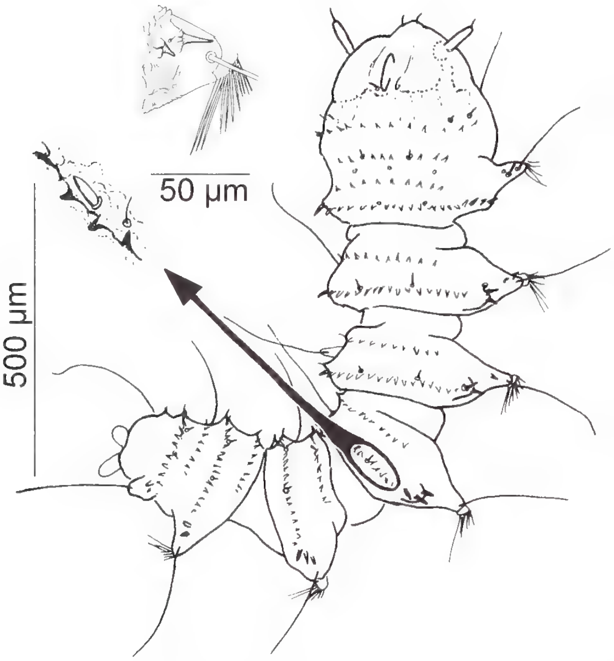

Fig. 13: *Philorus levanidovae* sp. n., first instar larva, dorsal view. Habitus with enlarged insets of dorsolateral armature and of apex of pseudopod (large seta clipped).

Comparisons. Because larvae of *P. levanidovae* and *P. chosenensis* cannot presently be distinguished, specimens from a tributary to Vodopadnaja River are tentatively assigned to *P. levanidovae* which is the sister-species of *P. chosenensis* Kitakami from Middle Korea; see there for distinction of males and pupae. Members of the so-called *Euliponeura*-group and *P. vividis* Kitakami have very similar pupae with medially meeting respiratory organs with low, crest-like lamellae and a spiracular slit with visible spiracular pore. Larvae of this group have similar dorsal armature; Japanese species are distinguished by forwardly shifted gills visible in dorsal view.

First instar larvae of *P. levanidovae* agree with *P. vividis* (KITAKAMI 1931, fig. 2) and *P. taiwanensis* Kitakami (KITAKAMI 1941b, fig. 2), but figures of the latter two species are not sufficiently detailed to compare integumental ornamentation.

Habitat. Kravtsovka stream flows in a narrow canyon shaded by forest; it forms many rapids and cascades. *Philorus levanidovae* was the only species of Blephariceridae found in the stream, larvae and pupae were collected from the hygropetric zone on big boulders, only a few larvae were found on pebbles in the main flow. Adults were swept from riverside vegetation. The small tributary to Vodopadnaja River flows in the shade of the forest edge; the collecting site was a few meters before the stream enters the Vodopadnaya River. Specimens were fully submerged in the main flow of the streamlet in which there were no other Blephariceridae. Conversely, no specimen of *P. levanidovae* was taken at a few meters distance in the fast-flowing unshaded Vodopadnaja river where *Agathon, Bibiocephala* and *Blepharicera* were common. The simultaneous presence of all life stages may suggest several overlapping generations, like in *P. chosenensis.*

Etymology. We are pleased to name this new Russian species in the honour of the late Dr. Iya M. LEVANIDOVA, Vladivostok, much admired pioneer scientist and grand old lady of Far East Russian freshwater research.

4.3.2. *Philorus chosenensis* Kitakami, 1931

Philorus chosenensis Kitakami, 1931 (KITAKAMI 1931: 93); 1950 (KITAKAMI 1950: 64, figs. 40-43).

Material. Lectotype (present designation) adult male, paralectotypes 1 pupa, 1 last instar larva (ZFMK); syntypes from Mt. Geumgang, Gangwon-do (= "Mt. Kongo"), Middle Korea, 25.VII.1939. – Additional material: 1 adult male, 1 pupa, 1 last instar larva (USNM), authentic material identified by Kitakami, possible syntypes.

P. chosenensis is thermophilic, hygropetric and plurivoltine (KITAKAMI 1950). The species is very similar to *P. levanidovae;* we saw no females. Males can be distinguished by the genitalia; Kitakami's figure is correct but too small to recognize details and consequently we provide a new illustration (Fig. 14). The above specimens appear to be all that still exist from Kitakami's collection and those that are definite syntypes are here designated as lectotype and paralectotypes, respectively. Only characters distinguishing *P. chosenensis* from *P. levanidovae* sp. n. are redescribed.

Adult. Male genitalia (Fig. 14): Dorsal branch of outer dististyle with broad but very blunt basal projection; apex short, rounded, not overhanging. Apex of ventral branch flat, resembling curved ribbon whose microsculpture changes from basal microtrichia to apical spinules but medial and lateral faces are similar. Inner dististyle sinuous, apex curved mediad, not dorsad. Penis of male in USNM is erect; parameres with small ovoid terminal section, enlargement being in parasagittal plane.

Pupa. Similar to *P. levanidovae* except fine but dark and distinct granulation.

Larva. Similar to *P. levanidovae*, no distinctive characters known.

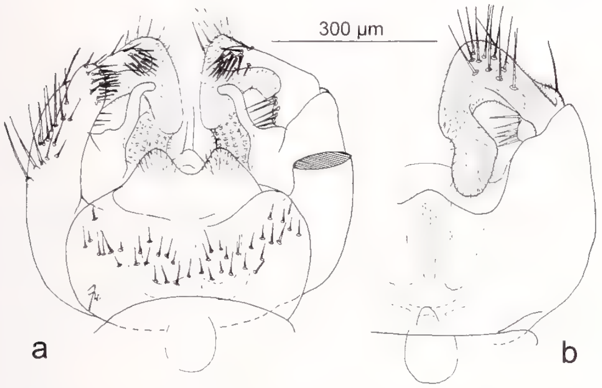

Fig. 14: *Philorus chosenensis* Kitakami, male lectotype. a, genitalia, dorsal view, left finger-shaped process cut; b, same, right half, ventral view.

4.4. Genus *Blepharicera* Macquart, 1843

Blepharicera Macquart, 1843 (MACQUART 1843: 61). Type species: *Blepharicera limbipennis* Macquart, 1843, by monotypy, a junior synonym of *Asthenia fasciata* Westwood, 1842.

Blepharicera is the most widespread genus of the family. It falls into several species groups (ZWICK 1990, ZWICK & ZWICK 1998) of which only the *fasciata*-group occurs in East Asia. The single species from the Russian Far East is new to science.

4.4.1. *Blepharicera parva* sp. n. (Figs. 15, 16)

Material. Holotype, 1 pharate ♂, paratypes 5 pharate ♂, 9 ♀, River Manoma, basin River Anjui [a tributary of Amur River], leg. Arefina & Tiunova, 28.07.1996; the same sample also includes 31 P, 30 L3 & L4 which have no status as syntypes (leg. IBSSAN; presently in PZ). Additional material: RFE03, 115 L1-L4; RFE09, 25L1, 67L2, 85L3, 137L4, 34P; RFE56, 42 L2-L4 (incl. prepupae); RFE10, 4 L1-L3; RFE21, 9 L1-L2; RFE28, 1 L2, 1L3; RFE37, 1 L3; RFE48, 39 L1-L3; RFE54, 29 L2-L4 (incl. prepupae) (all in PZ).

Primorje: Lazovskii Reservation, Lazovka River near vill. Lazo, leg. Vshivkova, 05.07.1978, 4L (IBP>PZ); 08.07.1979, 2P, 1L (IBP>PZ). Lazovsky Reserve, Kievka River, 04.08.1985, leg. Gostyukhina, 5L, 2P; 13.06.1998, leg. Arefina, 72L, 2P (IBSSAN). Ussuri River Basin, Zubkin Stream, 27.07.1992, leg. Tiunova, 1L (IBSSAN). Ussuri River near mouth of Izvilinka River, 08.08.1979, leg. Levanidova, 10L (IBSSAN). Ussuri-Bolshaya Ussurka River Basin, Perevalnaya Stream, 06.08.1997, leg. Tiunova, 4L, 2P (IBSSAN). Yedinka River (middle part), 14.08.1986, leg. Korionov, 3L, 7P (IBSSAN). Narva River (lower part), 02.08.1987, leg. Teslenko, 4L, 3P; 14.08.1994, leg. Arefina, 2L, 9P; Sikhote-Alin Reserve, Bystraya Stream, 02.08.1997, leg. Tiunova, 7L, 10P (IBSSAN).

Khabarovsk Territory: Iski River, 12.08.1959, leg. Levanidova, 5P, 3L (IBSSAN). Bikin River Basin near mouth of Omorochka Stream, 30.07.1995, leg. Tiunova, 1♀ (IBSSAN). Bikin River Basin, Klyuchevaya Stream, 28.07.1995, leg. Tiunova, 1L (IBSSAN). Bikin River Basin, Zeva River (upper part), 17.07.1995, leg. Tiunova, 1L (IBSSAN). Bikin River Basin, Zeva River, near Beriozovaya Stream, 24.07.1995, leg. Tiunova, 10L, 8P (IBSSAN). Bolshekhekhtsirsky Reserve, Ussuri River Basin, Bychikha Stream (15.5° C), 22.06.1958, leg. Levanidova, 4L, 1P (♀) (IBSSAN) (all in PZ).

A typical *Blepharicera*. Adults available only as pharate specimens; dimensions, pigmentation and details of wing therefore unknown.

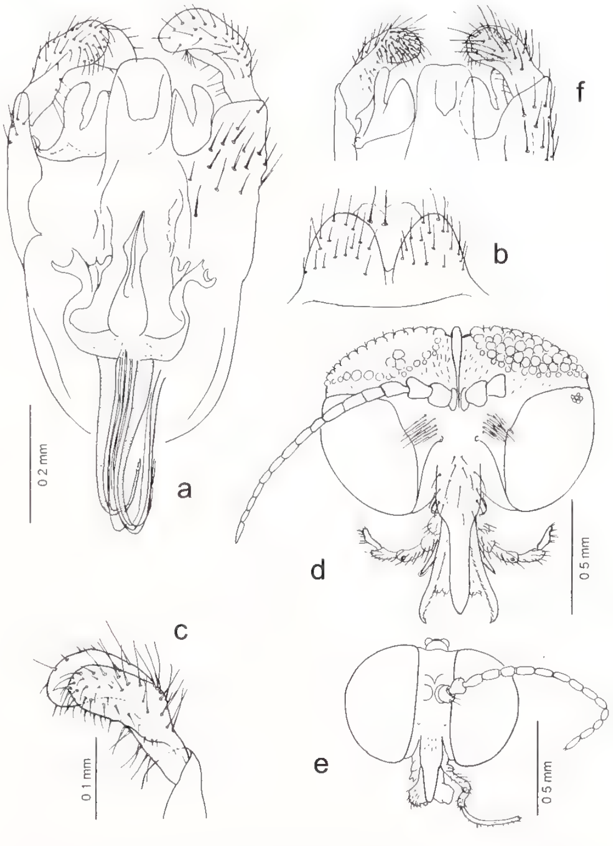

Fig. 15: *Blepharicera parva* sp. n., adults. a, b, male genitalia, dorsal view, tergite and cerci shown separately; c, left dististyle, dorsal; d, head of female; e, head of male; f, *Blepharicera japonica*, part of male genitalia, dorsal (from ZWICK 1990).

Adult. Male. Widely separate almost simple eyes, reduced upper portion forms narrow section at mesal rear margin of eye, behind ocelli. Rostrum shorter than head height, labella projecting slightly beyond labrum. No mandibles, hypopharynx, lacinia; palpal segments short except whip-like 5th segment. No facial pilosity. Antenna slender, most segments more than twice as long as wide. Coxae normal, simple. No tibial spurs. Tarsal claw falcate, with some hairs on sides near base.

Hypopygium slender, inner sclerites inverted as typical of *B. fasciata*-group. Tegmen lightly sclerotized, apex of common spade-shape. Inner diststyle divided into blade-like median and short finger-shaped lateral portions. Inner edge of outer diststyle with some basal setae, distally angularly bent mediad. Dorsal and ventral distal lobes deeply divided, dorsal lobe a bit angled and much shorter than the more regularly curved soft ventral lobe with medially projecting apex. Cercus narrowly rounded, no angles in contour.

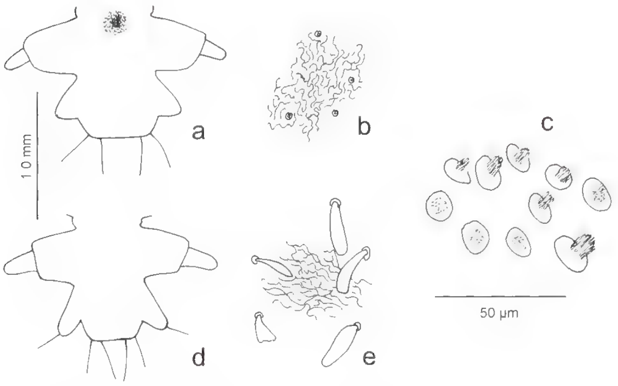

Fig. 16: *Blephariсera parva* sp. n. (a-c) and *B. japonica* (d, e). a, d, terminal body division of last instar larva, dorsal; b, e, details of integument on some middle abdominal segment; c, granula on abdominal segment of pupa. Figures a and d and c-e are to the same scales, respectively.

Female. A very narrow crest between eyes runs to ocellar triangle which is not raised. Bare strip separates unequal portions of widely separate eyes. Upper portion in frontal view slightly smaller than lower, convex, very large bulging ommatidia in centre, lateral ones much smaller. Antenna short, of 15 segments, acutely pointed, setiform, each flagellar segment with single longer seta on outside, resulting in sparse setal fringe. Distinct facial hair patch between base of antenna and base of rostrum. Rostrum about as high as head. Mandibles serrate, long, apex curved mediad. Hypopharynx serrate, hidden behind labrum which is little longer than labella. Lacinia distinct. Palpus segments short, especially 5th. Mesocoxa with usual hairy appendage. Hind tibia with two small unequal spurs, base of hind tarsus with some procumbent long black setae. Tarsal claws as in male. Genitalia not distinctive, three spherical receptacles with sclerotized duct whose diameter widens abruptly short distance from receptacle.

Pupa. Shape and respiratory organs typical of genus, 3.8-4.8 mm long, 2.0-2.5 mm wide. Integument glossy, dorsal granules on metathorax and abdomen tiny, each with central dome of closely packed hair-like pegs (Fig. 16c). Anterodorsally on abdominal tergites granules aggregate and form slightly raised warts. Anterior and posterior lamellae of gills of same width and almost twice as wide as lamellae 2 and 3 between them. Brown, also all four gill lamellae of same colour.

Larva. Last instar larvae up to 6.5 mm long, typical of subgroup. Cephalic sclerites with usual mottling but each dark spot on raised area of integument, which is hemispherical on medial frontal sclerite, but flat and obliquely rising from low front to high posterior edge on lateral frontal sclerites. Antenna two–segmented, segments separated by pale section of same length as basal segment, latter distinctly shorter than apical segment. Each abdominal tergite may have anteromedian wart, surrounding integument and intercalary segments darker than rest of surface; although some specimens lacking warts altogether. Surface finely microreticulate, with numerous tiny insertion points; setae reduced to tiny acutely conical pegs and not easily visible. Soft pale hairs on sides of body. Ventral face of body with distinct but pale asperities between sucker and base of pseudopods. Seven gill filaments in each tuft. Body divisions medially brownish, anterior part of each division darker than posterior, pale mark at paramedian muscle attachments; neck–pieces and lateral portions of divisions pale.

Last body division with truncate sclerotized blackish distal edge. Lateral lobes of segment bluntly triangular, their posterior contour meeting body contour at right angles. Last pseudopod reduced to sclerotized area around setal insertion, medial edge of sclerite often downcurved to form small grapple.

Larval instars 3, 2 and 1, respectively, with five, three and no gill filaments, less distinctly patterned, dull grey, lobes of last body division less distinct. Antenna one–segmented in instars 1 and 2, with very short dark ring representing basal segment only in instar 3. Cuticular ornaments of first instar larva as described for *B. fasciata* (ZWICK 1980), that is, only single prothoracic transverse cuticular crest present on thorax.

Variation. The only variation concerns the expression of tergal warts and dorsal pilosity in larvae. In some populations, especially at the type locality, warts are shallow and inconspicuous; in most others, particularly in the Kievka river, warts are steeply rising and high. Similar variation is known in other species, for example *B. fasciata*. While some specimens appear almost bare, others are fairly pilose. However, this may depend less on absence or presence of hairs than on extent of bacterial and detrital coating which greatly affects visibility of hairs.

Distinction from related species. On the Asian mainland occur only species of the *fasciata*-subgroup, which were all redescribed by ZWICK (1990). However, *B. japonica* Kitakami, 1931 is the only species of which all stages and both sexes are known (KITAKAMI 1931, 1950).

B. yamasakii (Kitakami, 1950), from Manchuria: Adults are very similar to *B. parva*, but both sexes bear a hairy appendage on mesocoxa (in all other species, present only in females). The upper portion of the female eyes are "nearly flat", and the sides of the lower division are "nearly vertical" whereas in *B. parva* both divisions are distinctly convex. The pupa is not recognizably different. The larva differs by the dense pale pilosity and lack of integumental warts although the shape of the caudal body division is similar to *B. parva*.

B. japonica: Adults resemble *B. parva*, but the male cerci are slightly pointed, the upper lobe of the outer diststyle is smaller than the lower (opposite in *B. parva*), and the lobes are shallowly separate. Females lack a hairy mesocoxal appendage but the trochanter is covered in dense black hairs. Eyes are simple, with no facial hair patches, and the rostrum lacks mandibles and hypopharynx. The width of the sclerotized receptacular duct changes gradually, not abruptly. *Blephariceera japonica* females have very slender, thin, skinny tarsi with strongly oblique articulations and heavy strongly curved claws; these details were previously overlooked. A similar character syndrome was recently noticed to be common in another tribe, Apistomyiini (ZWICK 1998). Pupae of *B. parva* and *B. japonica* can presently not be distinguished. Long lateral lobes of segment seven of *B. japonica* larva are directed obliquely backward (Fig. 16d). The surface bears pale, club-shaped flattened hairs among microreticulation (Fig. 16e) and no integumental warts. Three dark bands run over entire length of body. Cephalic sclerites are smooth, not sculptured as in *B. parva*. Instar 3 of *B. japonica* has already two distinct antennal segments, instar 2 possesses a small dark basal ring; otherwise not distinct from *B. parva*.

B. yankovskyi (Alexander, 1953): The single male from North Korea has very large eyes; the upper section is small but much less reduced than in *B. japonica*, and hence also different from *B. parva*.

B. dimorphops (Alexander, 1953) (from China, Fukien): Outer male gonostyle is very deeply divided, with both lobes slender, and this form is distinctly different from *B. parva* (figs. 8a-c of ZWICK 1990).

4.4.2. *Blepharicera* sp.

Material. Mongolia, Selenge, Mandal, Khonin Nuga [49°05'260N, 107°17'440E], Eroo River, 21.VI.2003, 1L3, 2L2, leg. P. Surenkhorloo (PZ).

The larvae resemble *B. parva*, but we are not certain of their conspecificity.

4.5. Genus *Neohapalothrix* Kitakami, 1938

Neohapalothrix Kitakami, 1938. Type species: *Neohapalothrix kanii* Kitakami, 1938, by original designation (KITAKAMI 1938: 341).

Asiobia Brodsky, 1954. Type species: *Asiobia acanthonympha* Brodsky, 1954, by original designation (BRODSKY 1954: 245). Synonymy of ZWICK, 1990: 253.

The phylogenetic status of the closely related genera *Neohapalothrix* and *Hapalothrix* (Europe; ZWICK, 1997b) is not firmly established because of conflicting characters. A dorsal larval feeler with geminate setae occurs only in Blephariceriini. ZWICK (1992) therefore included both genera in this tribe, assuming convergence for reduced wing veins and habitus characters. Most authors, however, regarded both genera as Paltostomatini because of reduced wing venation, curved front femora, short front and middle and very long hind legs. The labial brush here described for *Neohapalothrix* has so far only been observed in Paltostomatini (ZWICK 1998). In view of this last character we now assume that the genus actually belongs in that tribe. If so, the dorsal feeler must have evolved independently from Blephariceriini. Indeed, the feeler originates through splitting of the pseudopod, and is positioned in front of the pseudopod, not above it as is typical of Blephariceriini. Both traits are unique.

Neohapalothrix is endemic to Asia. The genus includes the type-species from Honshu and the widespread *N. manschukuensis* (Mannheims).

4.5.1. *Neohapalothrix manschukuensis* (Mannheims), 1938 (Figs. 17-20)

Curupira manschukuensis Mannheims, 1938. – Type-locality: Weischache, Manschukuo [China, Manchuria] (MANNHEIMS 1938: 329).

Asiobia acanthonympha Brodsky, 1954. – Type-localities: Russia: r. Angara, Padun; S-Primorje: r. Bikin; Kazakhstan: Altai, r. Bija (BRODSKY 1954: 250). – Synonymy of Zwick, 1990: 253.

Neohapalothrix shirozui Saigusa, 1973: 226. – Type locality: Japan, Hokkaido, Teshio, Piuka (SAIGUSA 1973: 226). – Synonymy of ZWICK, 1997b.

Curupira manschukuensis was described from a single female and tentatively placed in the neotropical genus *Curupira*. In the same year, KITAKAMI erected the genus *Neohapalothrix* for his new species, *kanii*, from Japan. Subsequently, KITAKAMI anticipated and established, respectively, the correct generic combination of the mainland species (KITAKAMI 1941a, 1951). However, it was later described and named two more times. BRODSKY (1954) presented all life stages. The amazing male tarsal structures were again illustrated by SAIGUSA (1973) and ZWICK (1997b) who also described changes in pseudopod structure between larval instars, comparing them with *Hapalothrix*.

Neohapalothrix manschukuensis was known from the Altai (BRODSKY 1954) and the Russian Far East; the new Mongolian record is therefore not surprising. The new record from Sakhalin closes a gap in the distribution, because a single male was taken on Hokkaido (SAIGUSA 1973). *Neohapalothrix manschukuensis* is common in the Russian Far East, conspecificity of all stages is definitely established through the metamorphotype-approach. We describe previously unknown details and present some ecological observations.

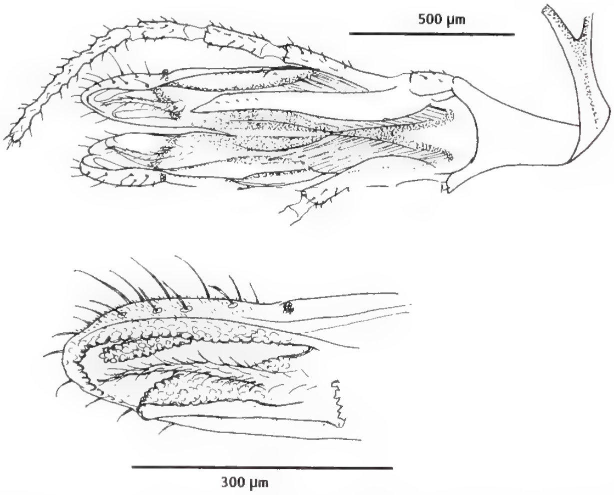

Fig. 17: *Neohapalothrix manschukuensis*. Female maxillolabium, dorsal view, and enlarged detail of left half of figure. Muscles diagrammatic.

Material (all in PZ). RFE09, 21P, 12L4; RFE14, 33L3, 64L2, 6L1; RFE15, 100L4, 36L3, 5L2, 3L1; RFE16, 4♂, 18♀, 20P, 5E, 18L4; RFE18, 43P, 8L4, 1L3; RFE19, 12L3; RFE21, 28L4, 84L3, 4L2; RFE23, 61P, 33L4, 3L3; RFE28, 24L4, 14L3, 1L2; RFE30, 88P, 13L4; RFE33, 341P, 19L4, 2L3; RFE35, 7P, 29L4, 1L2; RFE38, 23L4, 3L3; RFE39, 37P, 21L4; RFE47, 39L4, 2L3; RFE48, 3P, 50L4, 7L3, 1L1; RFE52, 1P; RFE53, 2♂; RFE56, 9P, 5L4, 1L3. Russian Far East, Sakhalin: Tym River at Ado-Tymovo Village, 10.07.1985, E. Makarchenko, 1 L4 (TA).

Additional material: Mongolia, Selenge: Mandal, Khonin Nuga [49°05'260N, 107°17'440E], Eroo River, 21.VI.2003, 28P, 43L4, 1L3; 25.VI.2003, 35♀; Eroo River [49°05'N, 107°17'E], 26.VI.2003, 2♀; 13.VII.2003, 2♀; Eroo hot spring, Irchleh River, [49°05'N, 107°17'E], 28.VI.2003, 16L4, 8P; Mandal, Ataa River, 18.VII.2003, 1L3; Mandal, Bar-Chuluut River [48°58'638N, 106°57'013E], 13.VII.2003, 2♀; Mandal, Bar-Chuluut River [49°02'784N, 106°58'669E], 09.VII.2003, 1L4 (all leg. P. Surenkhorloo; in PZ).

Adults. Both sexes of similar habitus. Female front femur slightly less sinuous than male. Female holoptic, eye little smaller than in male but also sharply divided into upper and lower portions. Rostra differ little, except longer maxillo-labium with base bent back distinctly only in females. Labella alike in both sexes. Soft scaly inner face forms anterior finger-shaped fold and larger posterior lobe with flat smooth medial face. Delicate brush at base of posterior lobe formed by slender cone with hair-like outgrowths of cuticle.

Female genitalia remarkable for short palpus-like apex of cercus not extending backward beyond general contour line. Oviscapt with truncate deeply divided but narrowly adjacent lobes. Dorsal face of each lobe without cover, side forming lateral wall ending in small dorsal angle. Sclerotized base of oviscapt truncate with prominent corners, almost bifid. Median of three pear-shaped black receptacles slightly smaller, all with short straight stalks.

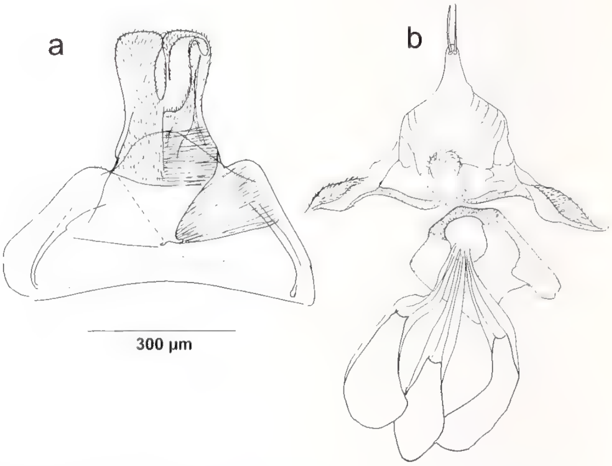

Fig. 18: *Neohapalothrix manschukuensis*, female genitalia. a, sternite 8 and oviscapt; muscles diagrammatic, as seen by transparency; left half of figure shows oviscapt in ventral, right half in dorsal view. b, sclerites from female genital cavity, with attached receptacles.

Larval instars. First instar larva (Figs. 19a-c) of normal habitus, dorsal side convex, rounded. Anal body division semicircular, no lobes; pseudopod seven represented only by tiny wart with long seta. Long, flattened cuticular structures resembling blunt hairs stand in transverse rows across body. One long row per thoracic segment. Each abdominal segment with short anterior plus long posterior row. Slender hair-like tergal and subtergal sensilla standing in posterior rows recognized by insertion points only at magnification over 200. Pseudopods in dorsal view largely hidden under body.

Base of each pseudopod with group of three spine-like cuticular outgrowths and a large seta (tergopleural and/or pre-dorsopseudopodal sensilla, HOGUE 1978), geminate setae (dorsopseudopodal setae of HOGUE 1978) typical of first instar pseudopods close to apex. Colourless delicate cuticular tube everted from tip of pseudopod with about 10 tiny sharp hooks at end. Antenna 1-segmented. No gills. Lateral rectal tubules very long, median ones minute.

Second instar larva with hard central cone on each abdominal segment. Integument with long curved hairs, some blunt, others apically thinned and finely pointed. On sides of body also short transparent spatulate and curved setae. Pseudopods forked (Fig. 19d), long posterior branch with rough ventral sole and three long dorsal setae. Short anterior branch with two or three long hairs in addition to geminate setae; ventrally smooth. Antenna 2-segmented. Single gill filaments, rectal tubules unchanged.

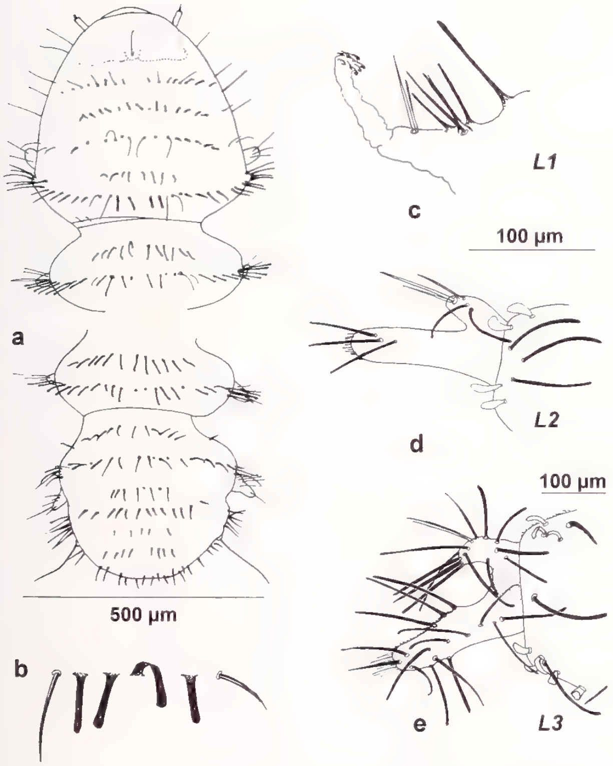

Fig. 19: *Neohapalothrix manschukuensis.* a, first instar larva (cephalic division plus abdominal segment 3; abdominal segments 5 and following); b, detail of dorsal armature, not to scale. Left side of abdominal segment three and pseudopod: c, first instar, posterior view (from a slide mount); d, e, 3rd and 4th instar, respectively, dorsal views. Same scale for c and d.

Branches of pseudopod deeply separate in 3rd (Fig. 19e) instar larva, completely divided in 4th instar. Hair cover denser, four and seven gill filaments, respectively. Abdominal segments 1-6 with strong dark dorsal spine on raised middle portion; body cross-section resembles equilateral triangle (lateral view in BRODSKY 1954 is far too flat!). Dorsal side sometimes (3rd instar) or normally (4th instar) patterned in dark brown and yellowish. Extent of pale pigment varies from only abdominal segments one and two and sides of five and six pale to mainly light specimens with dark cephalic sclerites, spines and pseudopods, and brown segments three and 4.

Ecological notes. Scientists of IBSSAN repeatedly picked numbers of adults from flowers of *Angelica saxatile* (Turcz.) (Daucaceae) and *Filipendula palmata* (Pall.) (Rosaceae). During our field work, adults were observed flying over the river banks, just before complete darkness. Dying and dead spent females were found between pebbles in stagnant water along the Khor River below Sukpai. Females seemed to have oviposited in areas where the river was receding. Individual last instar larvae and pupae observed on pebbles in the same area were alive but thickly covered with mud. Normally, larvae and pupae were found completely submerged, in strong current.

There is an obvious preference for large watercourses and potamal habitats. Population structure varied much between samples taken almost simultaneously. At several localities, water temperature was recorded at 20 min intervals (Gemini Tinytag datalogger ®) over night, between 19:00 and 8:00 hrs. The relationship between nocturnal minimum temperature and predominant developmental instar is shown in Figure 20; accelerated development in warm water is obvious. The sample from Komissarovka River is an exception but may be too small for safe judgement.

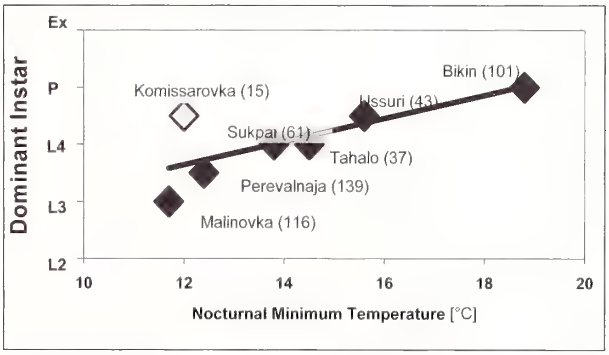

Fig. 20: *Neohapalothrix manschukuensis*, dominant instars (larval instars L2-L4, P = pupae, E = exuviae) in samples from rivers with different nocturnal minimum temperature, 11-24 June, 1998. Figures in parentheses are numbers of specimens in the sample.

Acknowledgements. We acknowledge the loan of important historical specimens and thank E.P. Nartshuk (Zoological Institute, Academy of Sciences, St. Petersburg), H.Ulrich and B. Sinclair (Museum Alexander Koenig, Bonn), W. Mathis (United States National Museum, Washington) and G.W. Courtney (Ames, Iowa) for their courtesy. G.W. Courtney and B. R. Stuckenberg (Pietermaritzburg) reviewed the final draft of the present study. K. Tanida (Osaka) supplied and partly translated a rare study by S. Kitakami. K.N. Satake kindly provided information on parts of the Kitakami collection in the Otsu Hydrobiological Station, Kyoto University. Prof. Y.J. Bae (Seoul) is sincerely thanked for providing transcriptions of Korean localities originally published in Japanese.

Interest in the Far East Blephariceridae arose during study of many occasional samples of Russian Blephariceridae, collected by I.M. Levanidova and other workers at the Institute of Biology and Soil Science, Russian Academy of Sciences, Vladivostok, which I.M. Levanidova made available to P. Zwick. We cordially thank our friends and colleagues Tatyana and Michail Tiunov, Valentina Teslenko and Valera Lyubaretz for help and comradeship during successful field work in the Russian Far East, in June 1998, and for the gift of samples collected at other occasions. Our thanks are also extended to Oleg Timoshkin (Institute of Limnology, Russian Academy of Sciences, Irkutsk) and Vladimir Samokhvalov (Institute of Biological Problems of the North, Russian Academy of Sciences, Magadan) for collecting material. Travel grant Nr. 436 RUS 18/28/97 by Deutsche Forschungsgemeinschaft to P. Zwick is gratefully acknowledged. We also thank the Max-Planck-Society for a grant allowing T. Arefina to participate in the work at Schlitz.

The gift of a rich collection of Japanese net-winged midges by S. Uchida (Toyota) to P. Zwick is very much appreciated. Important comparative material from Mongolia was lent or given to us, respectively, by W. Horn and M. Paul, Sächsische Akademie der Wissenschaften zu Leipzig, Arbeitsgruppe Limnologie, Lengfeld, Germany, and P. Surenkhorloo, Ulan Bataar; V. Devyatkov (Ust-Kamenogorsk) kindly gave us a collection from Kazakhstan. We sincerely thank them all.

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Received: 22.06.2004
Accepted: 07.09.2004
Corresponding editor: B. J. Sinclair

Editorial

Dear Reader,

In August 2005, the Federal Secretary of Culture – from which we receive 25% of our funds - imposed on us a financial cut of € 109,000. As a consequence, we could not afford to continue publishing issues of Bonner zoologische Beiträge after the release of the double issue 53(1/2) in June. We regret that we had to ask authors and readers for even more patience than usual. Our aim is to catch up to the actual yearly schedule as soon as possible. Last year, we had sufficient manuscripts, but suffered from a crucial lack of financial means. There are good chances, that we can reach our goal in 2006.

Due to an unfortunate coincidence of technical problems and personal misunderstandings, some of the colour illustrations in the Clas-M.-Naumann-memorial issue have been printed in discontenting quality. We, editors and printers, apologise for any trouble and disappointments caused through this failure. In attempting to make amends, all colour illustrations are herein reprinted and placed at the end of this double issue, after p. 358. The authors will be provided with colour-corrected high resolution PDF files of their contributions.

Sincerely
Michael Schmitt

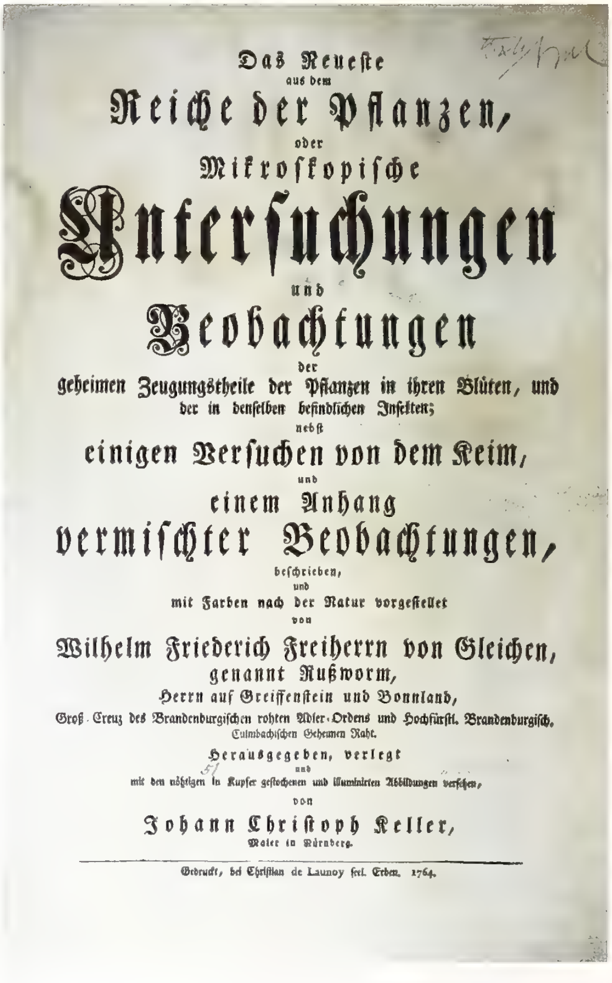
durch ihm Schloss Greiffenstein und die umliegenden Ländereien zugefallen waren; damals nahm er auch den Namen RUßWORM an. Sein Vermögen ermöglichte es ihm, sich nun ganz seinen Interessen zu widmen. Ein Schlüsselerlebnis war die Begegnung mit den „Mikroskopischen Augen- und Gemütsergötzungen" von Martin Frobenius LEDERMÜLLER und schließlich mit dem Autor dieses bis heute berühmten Werkes selbst. W. F. VON GLEICHEN besuchte M. F. LEDERMÜLLER 1760 in Erlangen und bestellte bei ihm ein Mikroskop, und Mikroskope sollten fortan auch zu seinen wichtigsten Arbeitsbehelfen gehören. Im Jahre 1762 hielt sich LEDERMÜLLER etwa vier Wochen bei VON GLEICHEN auf Schloß Greiffenstein auf, die beiden Mikroskopiker verbrachten offenbar eine glückliche Zeit, in der sie sich in gemeinsam erlebter Freude und Begeisterung ganz dem Mikroskopieren hingaben. Schon vor seiner Begegnung mit M. F. LEDERMÜLLER, unmittelbar nachdem er sich auf sein Schloss zurückgezogen hatte, hatte W. F. VON GLEICHEN eine rege Publikationstätigkeit begonnen, wobei er sich mit ganz unterschiedlichen naturwissenschaftlichen, landwirtschaftlichen und technischen Fragen befasste. Dass besonders diese frühen Publikationen manchmal eine genügend kritische Betrachtungsweise vermissen lassen, darf nicht unerwähnt bleiben. Ab 1760 wurde W. F. VON GLEICHEN ein Mikroskopiker ersten Ranges, ausgestattet mit einer ausgeprägten Beobachtungsgabe und einer ebenso ausgeprägten Lust, das Gesehene zu interpretieren, Schlüsse zu ziehen und zu veröffentlichen. So entstanden zahlreiche weitere Publikationen über sehr unterschiedliche naturwissenschaftliche Themen (Bibliographie: FIKENSCHER 1801).

W. F. VON GLEICHEN starb infolge eines Schlaganfalls in seinem 67. Lebensjahr am 16. (oder 18.) Juni 1783 auf Schloss Greiffenstein.

Die Bedeutung W. F. VON GLEICHENs als Naturforscher wurde schon zu seinen Lebzeiten erkannt, und schon unmittelbar nach seinem Tod erschienen Darstellungen seines Lebenswegs: WEIKARD 1783; ANONYMUS 1784; FIKENSCHER 1801. Von den späteren biographischen Publikationen über W. F. VON GLEICHEN sind vor allem die Arbeiten von WILLNAU (1926), WEIDNER (1980), GEUS (1989, 1990) und DETTNER (1997) zu erwähnen.

W. F. VON GLEICHEN war nicht nur ein begabter Experimentator, sondern ein ebenso talentierter Zeichner, der seine Publikationen mit vorzüglichen Abbildungen ausstattete. Seine berühmteste und durch hervorragend kolorierte Kupfertafeln ausgestattete entomologische Arbeit ist ohne Zweifel jene über die „Geschichte der gemeinen Stubenfliege" (VON GLEICHEN 1764), in der er überdies Beobachtungsfehler von M. F. LEDERMÜLLER aufzeigte, was bedauerlicherweise zu einer Entzweiung der beiden führte.

Entomologische Themen werden auch in mehreren anderen Publikationen VON GLEICHENs behandelt. In zwei Werken setzt sich VON GLEICHEN mit Neuropteren auseinander, nämlich in dem 1764 erschienene Band über „Das Neueste aus dem Reiche der Pflanzen ..." (Abb. 1) und in seinem 1770 publizierten „Versuch einer Geschichte der Blatläuse und Blatlausfreßer des Ulmenbaums ..." (Abb. 9). Das 1764 veröffentlichte Werk ist – wie man schon dem langen Titel („... und einem Anhang vermischter Beobachtungen ...") entnehmen kann – so etwas wie ein Sammelband über verschiedene Themen. Er enthält auch zwei neuropterologische Artikel, von denen der eine („Der Blatlausfreßer und seine Eier an einem Hanfblat") den präimaginalen Stadien einer Chrysopiden-Spezies, der andere („Die Hofdame") einer im Winter gefundenen Imago einer Florfliege gewidmet ist.



Das Neueſte
aus dem
Reiche der Pflanzen,
oder
Mikroſkopiſche
Unterſuchungen
und
Beobachtungen
der
geheimen Zeugungstheile der Pflanzen in ihren Blüten, und
der in denſelben befindlichen Inſekten;
nebſt
einigen Verſuchen von dem Keim,
und
einem Anhang
vermiſchter Beobachtungen,
beſchrieben,
und
mit Farben nach der Natur vorgeſtellet
von
Wilhelm Friederich Freiherrn von Gleichen,
genannt Rußworm,
Herrn auf Greiffenſtein und Bonnland,
Groß-Creuz des Brandenburgiſchen rohten Adler-Ordens und Hochfürſtl. Brandenburgiſch.
Culmbachiſchen Geheimen Raht.
Herausgegeben, verlegt
und
mit den nöhtigen in Kupfer geſtochenen und illuminirten Abbildungen verſehen,
von
Johann Chriſtoph Keller,
Maler in Nürnberg.

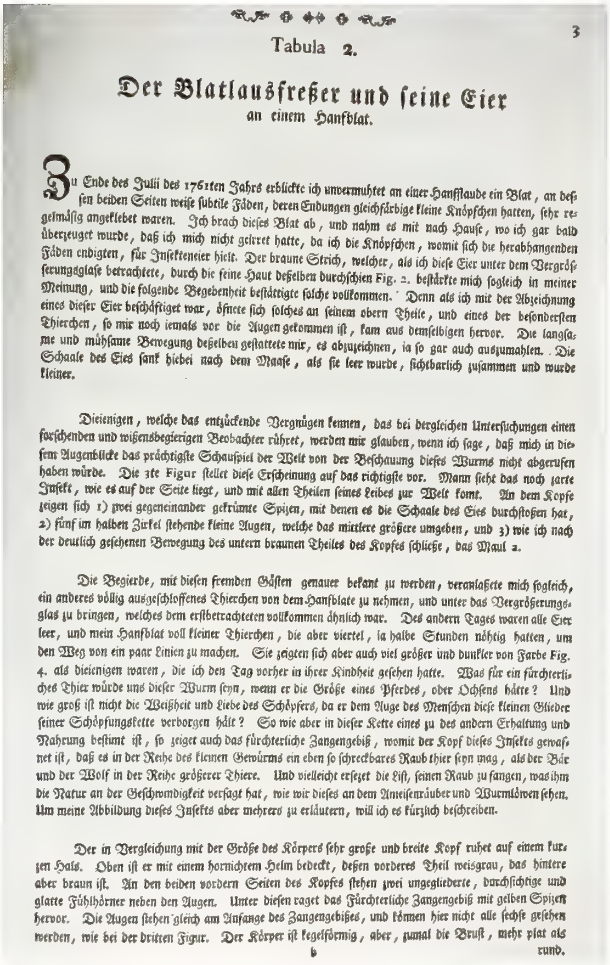
Gedruckt, bei Chriſtian de Launoy ſeel. Erben. 1764.

Abb. 1: W. F. VON GLEICHEN (1764), Titelblatt des Werks, das die Arbeiten über den „Blatlausfreßer ..." (1764a) und „Die Hofdame" (1764b) enthält (Bibl. H. & U. ASPÖCK)

In der 1770 veröffentlichten umfangreichen Arbeit wird die Biologie einer Hemerobiiden-Spezies ausführlich dargestellt. VON GLEICHEN hat sich wenig um die korrekte Bestimmung und Benennung der von ihm untersuchten Insekten gekümmert, vielmehr hat er einfache deutsche Namen verwendet. Sein Augenmerk konzentrierte sich ganz und gar auf die funktionellen Aspekte, auf Lebensweise und Entwicklung, während ihn taxonomische und systematisch Aspekte offenbar gar nicht interessierten. Geus (1990) zitiert eine geradezu abfällige Aussage von Gleichens über jene Naturforscher, „die nur Systeme ausheckten, von nichts als Nomenklatur, Papillons, Konchylien u.d.g. mit einem Worte, nur immer von der Schale der Dinge schwatzten. Solche Menschen setzen meistens die Naturkunde nur zu einem blossen Gedaechtniswerke oder blos zu einer leeren Liebhaberei herab.“

2. 1764A: „DER BLATLAUSFREẞER UND SEINE EIER AN EINEM HANFBLAT“ (ABB. 2-6)

In diesem Aufsatz schildert von Gleichen, wie er Ende Juli 1761 an einer Hanfstaude ein Blatt fand, „an dessen beiden Seiten weise subtile Fäden, deren Endungen gleichfärbige kleine Knöpfchen hatten, sehr regelmäßig angeklebet waren“. von Gleichen brach das Blatt ab, nahm es mit nach Hause und fand seine Vermutung, dass es sich bei den „Knöpfchen“ um Insekteneier handelte, bestätigt, als er bei Betrachtung der Knöpfchen unter dem Mikroskop die durchscheinende Larve sah und plötzlich Zeuge des Schlüpfens der Eilarve wurde. von Gleichen beschreibt Eier und Larven außerordentlich genau und bildet sie auch in hervorragender Weise ab; seine Zeichnungen dienten Johann Christoph Keller (1737-1795) als Vorlagen für die Kupferstiche (Abb. 2). Zu seinem Bedauern konnte er keine weiteren Zeichnungen anfertigen, weil die Larven nach drei Tagen tot und eingeschrumpft waren. Von Gleichen wusste zu diesem Zeitpunkt nicht, welche Insekten er vor sich hatte, was ihre Nahrung ist, ja er schreibt sogar ganz offenherzig: „Allein meine Ungewissheit ihrer Bestimmung verleitete mich, zu glauben, dass sie wenigstens nicht viel größer werden würden, als sie waren, da ich eines derselben Fig. 4. vergrößert abbildete.“ Erst nach dieser Untersuchung kam von Gleichen das berühmte Werk von Réaumur (1734-1742) in die Hände, in dessen drittem Band (1737) die Biologie von Chrysopiden beschrieben wird. Von Gleichen gibt auch unumwunden zu, dass er, hätte er von Réaumurs Werk vorher Kenntnis gehabt, mit seinen „Blatlausfreßern viel sorgfältiger umgegangen seyn würde“. Erst durch Réaumur erfuhr von Gleichen , dass die „Fresszangen“ nicht zum Fressen, sondern zum Saugen dienen und dass sie „hohl und an den Spitzen offen sind“. Dass diese Saugzangen von größter systematischer Bedeutung sind und das die Ordnung Neuroptera begründende Merkmal schlechthin (also in heutiger Terminologie: die Autapomorphie) der Neuroptera sind, wusste auch Réaumur nicht. Erst mehr als 100 Jahre später erkannte der junge Friedrich Brauer den außerordentlichen systematischen Wert des Merkmals, indem er alle Familien der Neuroptera (im heutigen Sinn) in einer Ordnung (er nannte sie damals Megaloptera) vereinte (Brauer & Löw 1857).



3

Tabula 2.

Der Blatlausfreßer und ſeine Eier
an einem Hanfblat.

Zu Ende des Julii des 1761ten Jahrs erblickte ich unvermuhtet an einer Hanfſtaude ein Blat, an deſſen beiden Seiten weiſe ſubtile Fäden, deren Endungen gleichfärbige kleine Knöpfchen hatten, ſehr regelmäſig angeklebet waren. Ich brach dieſes Blat ab, und nahm es mit nach Hauſe, wo ich gar bald überzeuget wurde, daß ich mich nicht geirret hatte, da ich die Knöpfchen, womit ſich die herabhangenden Fäden endigten, für Inſekteneier hielt. Der braune Strich, welcher, als ich dieſe Eier unter dem Vergröſſerungsglaſe betrachtete, durch die feine Haut deßelben durchſchien Fig. 2. beſtärkte mich ſogleich in meiner Meinung, und die folgende Begebenheit beſtättigte ſolche vollkommen. Denn als ich mit der Abzeichnung eines dieſer Eier beſchäftiget war, öfnete ſich ſolches an ſeinem obern Theile, und eines der beſonderſten Thierchen, ſo mir noch iemals vor die Augen gekommen iſt, kam aus demſelbigen hervor. Die langſame und mühſame Bewegung deßelben geſtattete mir, es abzuzeichnen, ia ſo gar auch auszumahlen. Die Schaale des Eies ſank hiebei nach dem Maaſe, als ſie leer wurde, ſichtbarlich zuſammen und wurde kleiner.

Dieienigen, welche das entzückende Vergnügen kennen, das bei dergleichen Unterſuchungen einen forſchenden und wißensbegierigen Beobachter rühret, werden mir glauben, wenn ich ſage, daß mich in dieſem Augenblicke das prächtigſte Schauſpiel der Welt von der Beſchauung dieſes Wurms nicht abgerufen haben würde. Die 3te Figur ſtellet dieſe Erſcheinung auf das richtigſte vor. Mann ſieht das noch zarte Inſekt, wie es auf der Seite liegt, und mit allen Theilen ſeines Leibes zur Welt komt. An dem Kopfe zeigen ſich 1) zwei gegeneinander gekrümte Spizen, mit denen es die Schaale des Eies durchſtoßen hat, 2) fünf im halben Zirkel ſtehende kleine Augen, welche das mittlere größere umgeben, und 3) wie ich nach der deutlich geſehenen Bewegung des untern braunen Theiles des Kopfes ſchließe, das Maul a.

Die Begierde, mit dieſen fremden Gäſten genauer bekant zu werden, veranlaßete mich ſogleich, ein anderes völlig ausgeſchloffenes Thierchen von dem Hanfblate zu nehmen, und unter das Vergrößerungsglas zu bringen, welches dem erſtbetrachteten vollkommen ähnlich war. Des andern Tages waren alle Eier leer, und mein Hanfblat voll kleiner Thierchen, die aber viertel, ia halbe Stunden nöhtig hatten, um den Weg von ein paar Linien zu machen. Sie zeigten ſich aber auch viel größer und dunkler von Farbe Fig. 4. als dieienigen waren, die ich den Tag vorher in ihrer Kindheit geſehen hatte. Was für ein fürchterliches Thier würde uns dieſer Wurm ſeyn, wenn er die Größe eines Pferdes, oder Ochſens hätte? Und wie groß iſt nicht die Weißheit und Liebe des Schöpfers, da er dem Auge des Menſchen dieſe kleinen Glieder ſeiner Schöpfungskette verborgen hält? So wie aber in dieſer Kette eines zu des andern Erhaltung und Nahrung beſtimt iſt, ſo zeiget auch das fürchterliche Zangengebiß, womit der Kopf dieſes Inſekts gewafnet iſt, daß es in der Reihe des kleinen Gewürms ein eben ſo ſchreckbares Raub thier ſeyn mag, als der Bär und der Wolf in der Reihe größerer Thiere. Und vielleicht erſezet die Liſt, ſeinen Raub zu fangen, was ihm die Natur an der Geſchwindigkeit verſagt hat, wie wir dieſes an dem Ameiſenräuber und Wurmlöwen ſehen. Um meine Abbildung dieſes Inſekts aber mehrers zu erläutern, will ich es kürzlich beſchreiben.

Der in Vergleichung mit der Größe des Körpers ſehr groſe und breite Kopf ruhet auf einem kurzen Hals. Oben iſt er mit einem hornichtem Helm bedeckt, deßen vorderes Theil weisgrau, das hintere aber braun iſt. An den beiden vordern Seiten des Kopfes ſtehen zwei ungegliederte, durchſichtige und glatte Fühlhörner neben den Augen. Unter dieſen raget das Fürchterliche Zangengebiß mit gelben Spizen hervor. Die Augen ſtehen gleich am Anfange des Zangengebißes, und können hier nicht alle ſechſe geſehen werden, wie bei der dritten Figur. Der Körper iſt kegelförmig, aber, zumal die Bruſt, mehr plat als

b rund.

Abb. 2: W. F. von Gleichen (1764a), Erste Seite der Arbeit über den „Blatlausfreßer ...“

Wahrscheinlich verdanken wir indes dem Umstand, dass von Gleichen das Werk von Réaumur nicht früher zur Hand hatte, die schön kolorierte Kupfertafel der Eier und der Erstlarve. (Die auf Fig. 5 und Fig. 6 dargestellten leeren Eier stammen von einem späteren Fund des Gärtners von Gleichens auf einer Zwetschke.) Unseres Wissens handelt es ich dabei um die erste farbige Darstellung einer Chrysopiden-Larve mit einer Wiedergabe des Pigmentierungsmusters in der gesamten entomologischen Literatur. Die Darstellung ist so genau, dass der Versuch, die Larve zu bestimmen, lohnend erschien. Die Larven fast aller in Mitteleuropa vorkommenden Chrysopiden sind gut bekannt, zu überwiegendem Teil existieren auch (allerdings nicht durchwegs

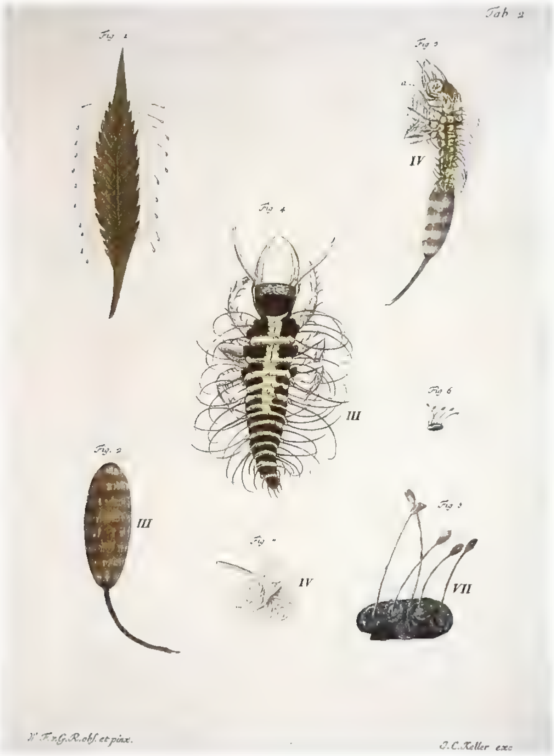


Abb. 3: W. F. VON GLEICHEN (1764a), Tafel zu der Arbeit über den „Blatlausfreßer ...“

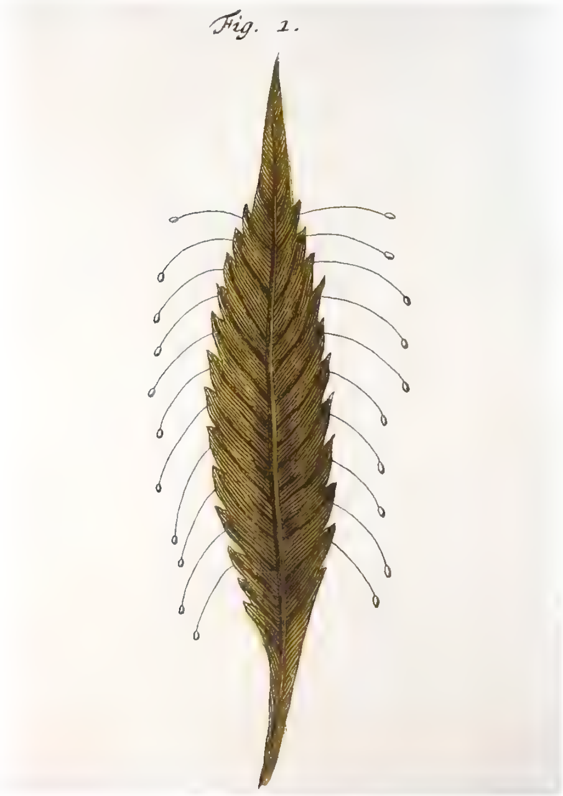


Abb. 4: W. F. VON GLEICHEN (1764a), Ausschnitt der Tafel zu der Arbeit über den „Blatlausfreßer ...“: Die in (für *C. pallens* charakteristischen) Reihen abgelegten Eier.

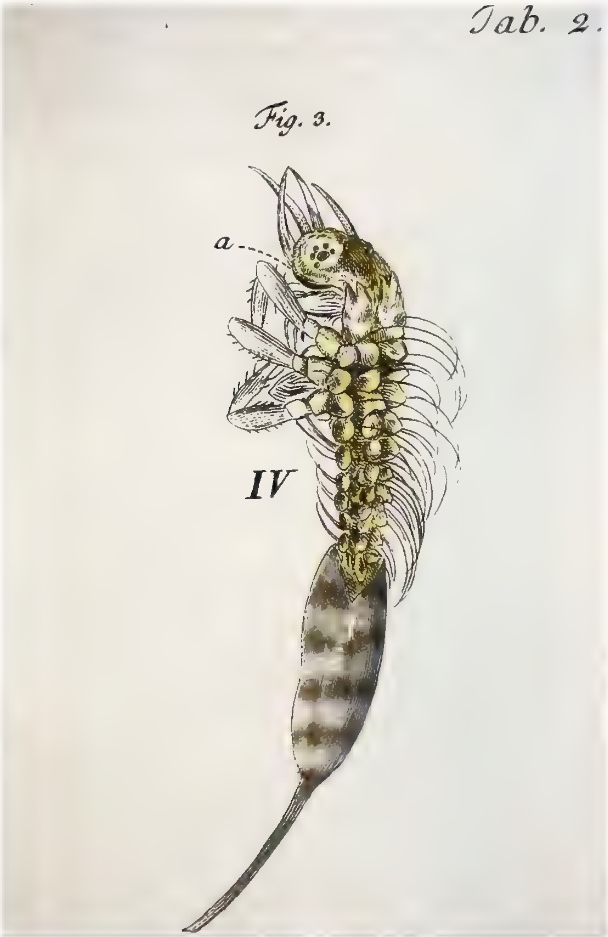

Tab. 2.
Fig. 3.
a
IV

Abb. 5: W. F. VON GLEICHEN (1764a), Ausschnitt der Tafel zu der Arbeit „Blatlausfreßer ...“: Die aus dem Ei schlüpfende Larve (von *C. pallens*).

auch vom ersten Larvenstadium) gute Abbildungen (vgl. KILLINGTON 1936-1937; PRINCIPI 1940; GEPP 1983; DIAZ-ARANDA 1992; DIAZ-ARANDA & MONSERRAT 1995). Vergleicht man die Larve VON GLEICHENs mit den verfügbaren Abbildungen, so findet sich die größte Übereinstimmung mit *Chrysopa pallens* (Rambur, 1838). Wir haben den derzeit vermutlich besten Kenner der präimaginalen Stadien von Chrysopiden, Herrn Prof. Dr. Peter DUELLI (Birmensdorf) um eine Beurteilung der Abbildung in VON GLEICHENs Arbeit gebeten. Nach seiner Meinung lassen die in Reihen abgelegten Eier sofort auf *C. pallens* schließen. Ebenso spricht die Pigmentierung der Kopfkapsel am ehesten für *C. pallens*. Weiters schreibt er: „Die langen, am Ende gebogenen Borsten lassen auf einen trash-carrier schließen. Das ist *C. pallens* ja nicht. Allerdings sind bei allen Chrysopiden-Arten die Borsten des ersten Larvenstadiums, relativ zur Körperlänge gesehen, viel länger als im 3. Larvenstadium. Auch tragen viele Arten dann doch noch etwas trash (debris) mit sich herum, später nicht mehr. Verglichen etwa mit *Chrysoperla*-Larven sind bei *C. pallens* auch bei der L3 die Borsten sehr lang." Zusammenfassend hält Prof. Duelli die Larven in von Gleichens Arbeit mit größter Wahrscheinlichkeit für *Chrysopa pallens.*

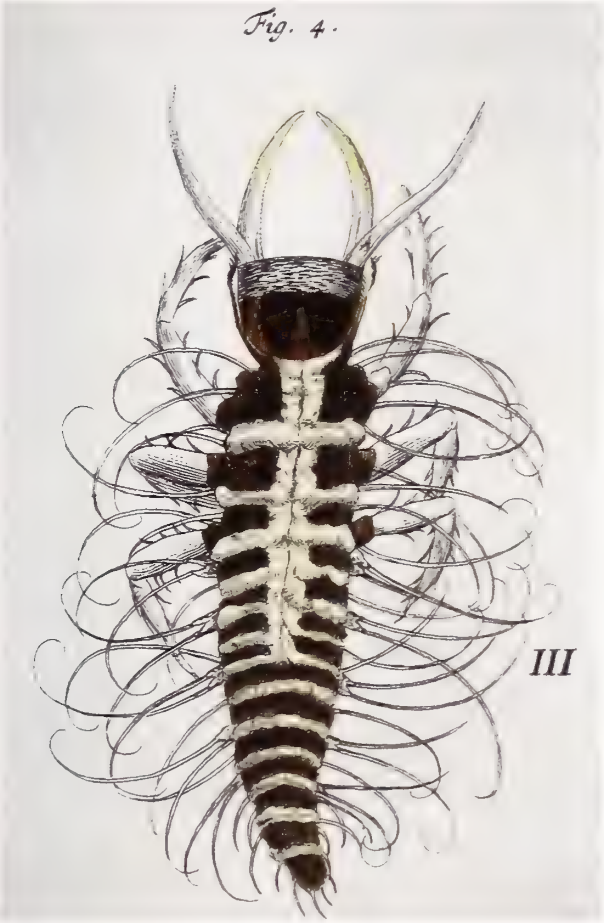


Abb. 6: W. F. von Gleichen (1764a), Ausschnitt der Tafel zu der Arbeit über den „Blatlausfreßer ....": Erstlarve (von *C. pallens*).

Diese Art (früher als *Chrysopa septempunctata* Wesmael, 1841, bekannt) ist eine extrem expansive, polyzentrische Art mit Ausbreitungszentren in der West- und in der Ostpaläarktis und einer Verbreitung, die nahezu ganz Europa (mit Ausnahme der nördlichen Teile, jedenfalls ganz Mitteleuropa von der Ebene bis in die kolline Stufe), NW-Afrika sowie weite (auch tropische) Teile Asiens östlich bis Japan und Taiwan umfasst (Aspöck et al. 1980; Aspöck et al. 2001). Mit Sicherheit war und ist die Art im Bereich des Rußworm'schen Schlosses, wie überhaupt in Franken, häufig. (Zur Verbreitung von *Ch. pallens* in Deutschland siehe Saure et al 2003.)

Diese durch die erste kenntliche Farbabbildung einer Chrysopiden-Larve und die Beschreibung des Schlüpfvorgangs bemerkenswerte Arbeit von Gleichens ist offenbar weitestgehend in Vergessenheit geraten. Selbst in der an Vollständigkeit kaum überbietbaren Bibliographie von Oswald (2004) fehlt sie. Ältere und z. T. sogar kolorierte Darstellungen von Chrysopiden-Larven finden sich u. a. bei Goedart (1669), Albin (1720), Frisch (1736), Réaumur (1734-1742), Bonnet (1745, Übersetzung: Goeze 1773), sie sind allerdings durchwegs grob ausgeführt und lassen jedenfalls keine Art-Bestimmung zu.

3. 1764B: „DIE HOFDAME" (ABB. 7-8)

Auch diese Arbeit mit dem ungewöhnlichen Titel fehlt in der Bibliographie von Oswald (l. c.), obwohl sie die vermutlich größte je publizierte Abbildung einer Chrysopide enthält.

Von Gleichen schildert in dem der Zeit entsprechenden narrativen Stil, wie sich „zur Zeit des Carnevals im Jenner bei später Nacht" ein Insekt auf eine Spielkarte setzte, das durch seine Schönheit auffiel (weshalb ihm von Gleichen den Namen „Hofdame" gab). Tags darauf untersuchte von Gleichen das Insekt mit freiem Auge ebenso wie unter dem Mikroskop und führte eine kolorierte Zeichnung aus, von der J. C. Keller einen Kupferstich anfertigte, den von Gleichen kolorierte.

Das Insekt ist von jedem Entomologen sogleich als Chrysopide zu erkennen, und jeder Neuropterologe weiß, dass es sich dabei nur um eine *Chrysoperla*-Art handeln kann. Die in Mitteleuropa vorkommenden Chrysoperla-Arten überwintern als Imagines, und unter diesen nehmen manche (in Mitteleuropa als einzige Chrysopiden) im Herbst eine gelblich-bräunlich-rötliche Färbung an. Vor 40 Jahren wäre die Bestimmung völlig problemlos erschienen. Damals kannte man nur eine einzige Chrysopiden-Spezies unter den Chrysopiden Mitteleuropas, die als Imago überwintert und im Herbst ihre Färbung von grün in braun verändert: *Chrysoperla carnea* (Stephens, 1836). Im Verlauf der vergangenen Jahrzehnte hat sich gezeigt, dass „die alte *Chrysoperla carnea*" nur als Kollektivnahme für mehrere morphologisch schwierig zu differenzierende Spezies zu betrachten ist, von denen mindestens 5 in Europa und z. T. auch in Mitteleuropa vorkommen (Literatur hierzu: Henry & Duelli 1999; Henry et al 1996, 2002; Henry et al 2003; Johnson et al 2003; Aspöck et al. 2001):

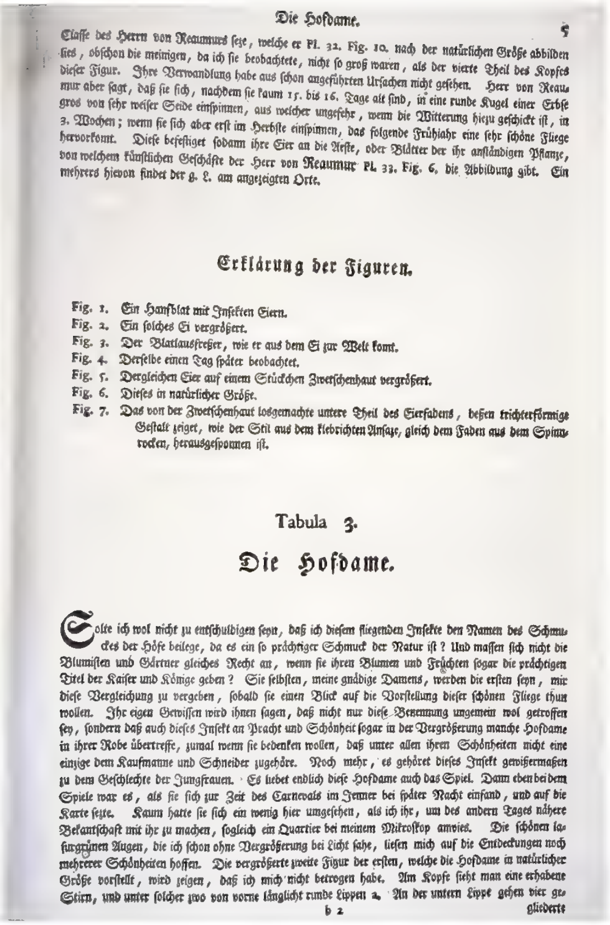
Chrysoperla carnea (Stephens, 1836)

Chrysoperla lucasina (Lacroix, 1912)

Chrysoperla mediterranea (Hölzel, 1972)

Chrysoperla pallida (Henry, Duelli & Johnson, 2002)

Chrysoperla agilis (Henry, Brooks, Duelli & Johnson, 2003).



Die Hofdame. 5

Claſſe des Herrn von Reaumurs ſeze, welche er Pl. 32. Fig. 10. nach der natürlichen Größe abbilden lies, obſchon die meinigen, da ich ſie beobachtete, nicht ſo groß waren, als der vierte Theil des Kopfes dieſer Figur. Ihre Verwandlung habe aus ſchon angeführten Urſachen nicht geſehen. Herr von Reaumur aber ſagt, daß ſie ſich, nachdem ſie kaum 15. bis 16. Tage alt ſind, in eine runde Kugel einer Erbſe gros von ſehr weiſer Seide einſpinnen, aus welcher ungefehr, wenn die Witterung hiezu geſchickt iſt, in 3. Wochen; wenn ſie ſich aber erſt im Herbſte einſpinnen, das folgende Frühiahr eine ſehr ſchöne Fliege hervorkomt. Dieſe befeſtiget ſodann ihre Eier an die Aeſte, oder Blätter der ihr anſtändigen Pflanze, von welchem künſtlichen Geſchäfte der Herr von Reaumur Pl. 33. Fig. 6. die Abbildung gibt. Ein mehrers hievon findet der g. L. am angezeigten Orte.

Erklärung der Figuren.

Fig. 1. Ein Hanfblat mit Inſekten Eiern.
Fig. 2. Ein ſolches Ei vergrößert.
Fig. 3. Der Blatlausfreßer, wie er aus dem Ei zur Welt komt.
Fig. 4. Derſelbe einen Tag ſpäter beobachtet.
Fig. 5. Dergleichen Eier auf einem Stückchen Zwetſchenhaut vergrößert.
Fig. 6. Dieſes in natürlicher Größe.
Fig. 7. Das von der Zwetſchenhaut losgemachte untere Theil des Eierfadens, deßen trichterförmige Geſtalt zeiget, wie der Stil aus dem klebrichten Anſaze, gleich dem Faden aus dem Spinnrocken, herausgeſponnen iſt.

Tabula 3.

Die Hofdame.

Solte ich wol nicht zu entſchuldigen ſeyn, daß ich dieſem fliegenden Inſekte den Namen des Schmuckes der Höfe beilege, da es ein ſo prächtiger Schmuck der Natur iſt? Und maſſen ſich nicht die Blumiſten und Gärtner gleiches Recht an, wenn ſie ihren Blumen und Früchten ſogar die prächtigen Titel der Kaiſer und Könige geben? Sie ſelbſten, meine gnädige Damens, werden die erſten ſeyn, mir dieſe Vergleichung zu vergeben, ſobald ſie einen Blick auf die Vorſtellung dieſer ſchönen Fliege thun wollen. Ihr eigen Gewiſſen wird ihnen ſagen, daß nicht nur dieſe Benennung ungemein wol getroffen ſey, ſondern daß auch dieſes Inſekt an Pracht und Schönheit ſogar in der Vergrößerung manche Hofdame in ihrer Robe übertreffe, zumal wenn ſie bedenken wollen, daß unter allen ihren Schönheiten nicht eine einzige dem Kaufmanne und Schneider zugehöre. Noch mehr, es gehöret dieſes Inſekt gewißermaßen zu dem Geſchlechte der Jungfrauen. Es liebet endlich dieſe Hofdame auch das Spiel. Dann eben bei dem Spiele war es, als ſie ſich zur Zeit des Carnevals im Jenner bei ſpäter Nacht einfand, und auf die Karte ſezte. Kaum hatte ſie ſich ein wenig hier umgeſehen, als ich ihr, um des andern Tages nähere Bekantſchaft mit ihr zu machen, ſogleich ein Quartier bei meinem Mikroſkop anwies. Die ſchönen laſurgrünen Augen, die ich ſchon ohne Vergrößerung bei Licht ſahe, lieſen mich auf die Entdeckungen noch mehrerer Schönheiten hoffen. Die vergrößerte zweite Figur der erſten, welche die Hofdame in natürlicher Größe vorſtellt, wird zeigen, daß ich mich nicht betrogen habe. Am Kopfe ſieht man eine erhabene Stirn, und unter ſolcher zwo von vorne länglicht runde Lippen a. An der untern Lippe gehen vier ge-

b 2 gliederte

Abb. 7: W. F. VON GLEICHEN (1764b), erste Seite der Arbeit über „Die Hofdame“.

Diese fünf Taxa unterscheiden sich vor allem durch spezifische Vibrationsmuster, die sich durch verschieden langes, durch unterschiedliche Intervalle und Folgen gekennzeichnetes Vibrieren mit dem Abdomen ergeben. Die Vibrationen werden auf das Substrat übertragen und erreichen über dieses andere Individuen, die die spezifischen Signale mit den Subgenualorganen der Beine wahrnehmen. Beide Geschlechter zeigen dieses der Partner-Findung dienende Verhalten, und wenn zwei Phäna mit unterschiedlichen Vibrationsmustern zusammentreffen, kommt es nicht nur nicht zur Paarung, in vielen Fällen ist sogar eine aggressive Reaktion die Folge. Die Taxa sind Spezies mit zum Teil unterschiedlich fortgeschrittener genetischer Isolierung. Sie werden häufig als „song-morphs“ bezeichnet. Unter experimentellen Bedingungen können Paarungen zwischen verschiedenen „song-morphs“ manchmal „erzwungen“ werden.

Ch. mediterranea und *Ch. lucasina* unterscheiden sich morphologisch hinlänglich und konstant von den anderen drei Spezies, deren morphologische Unterschiede gering sind. Alle genannten *Chrysoperla*-Arten überwintern als Imagines, aber nur drei von ihnen (*Ch. carnea, Ch. pallida, Ch. agilis*) verändern im Herbst die Färbung von grün zu rötlich-bräunlich-gelblich. Diese Färbung wird während der gesamten winterlichen Diapause bis zum nächsten Frühjahr beibehalten. Für die Deutung der Abbildung der „Hofdame“ (Abb. 8) VON GLEICHENS scheiden also *Ch. lucasina* und *Ch. mediterranea* jedenfalls aus.

Auch die in verschiedenen Teilen des Mittelmeerraums nördlich bis in die Südschweiz nachgewiesene *Ch. agilis* kann ausgeklammert werden, sie ist im übrigen bisher in Mitteleuropa nicht nachgewiesen worden und kommt mit großer Wahrscheinlichkeit in diesem Teil Europas tatsächlich nicht vor. Von den verbleibenden zwei Arten – *Ch. carnea* und *Ch. pallida* – gilt *Ch. pallida* als „Waldart“, die nur selten in Häusern überwintert. *Ch. carnea* hingegen ist ein ausgeprägter Kulturfolger und eine in allen Städten und Dörfern Mitteleuropas häufige Florfliege.

Auch in diesem Fall haben wir den führenden *Chrysoperla*-Spezialisten, Prof. Dr. Peter DUELLI (Birmensdorf), um seine Beurteilung des kolorierten Kupferstichs gebeten. Seine Antwort: „Die Färbung der Hofdame ist exakt das, was ich für *C. carnea* s. str. erwarten würde. Auch die Tatsache, dass sie im Januar im Haus anflog, spricht für *carnea*, *C. lucasina* ist wegen der Färbung ausgeschlossen, *C. pallida* (Waldart) kommt selten in die Häuser und ist etwas bräunlich-gelber im Winter“. Wir können also tatsächlich davon ausgehen, dass W. F. VON GLEICHEN die erste kenntliche – und überdies farbige – Darstellung jener Spezies veröffentlicht hat, die STEPHENS (1836) mehr als 70 Jahre später als *Chrysopa carnea* nomenklatorisch gültig beschrieben hat und die mit Sicherheit die in der Literatur am meisten behandelte Neuropteren-Spezies ist. *Chrysoperla carnea* ist zudem gewiss auch die am intensivsten und unter den verschiedensten Gesichtspunkten untersuchte Neuropteren-Art. VON GLEICHENS Abbildung ist – obwohl 240 Jahre alt – keineswegs die erste Abbildung einer Florfliege. Darstellungen von Chrysopiden findet man schon bei MOUFFET (1634), ALDROVANDI (1638), JONSTON (1657), GOEDART (1668), FRISCH (1736), RÖSEL VON ROSENHOF (1755), und natürlich bei RÉAUMUR (1734-1742) und bei BONNET (1745) und anderen früheren Autoren. Einige Autoren (GOEDART, ALBIN, RÖSEL VON ROSENHOF) haben sogar kolorierte Abbildungen veröffentlicht. Allerdings ist eine sichere Identifizierung der Art in keinem Fall möglich. Man muss jedoch gerechterweise erwähnen, dass drei Umstände die Identifizierung der von VON GLEICHEN dargestellten Florfliege ermöglicht haben: die genaue Kenntnis des Fundorts (Schloss Greiffenstein in Unterfranken), das Funddatum (Januar, aktiv im Haus) und die bräunliche (Ver-) Färbung des Tiers. Das Geäder hat VON GLEICHEN zwar sehr schön (und sogar – erstmals in der Literatur – mit doppelten Strichen), aber alles andere als richtig gezeichnet. Zu jener Zeit wusste man natürlich noch nichts über Geäder-Merkmale von Chrysopiden und deren systematische Bedeutung, weshalb man – das gilt geradezu für alle Autoren jener Zeit – auf eine korrekte Wiedergabe des Geäderverlaufs und der Zahl und Position der Queradern kaum achtete.

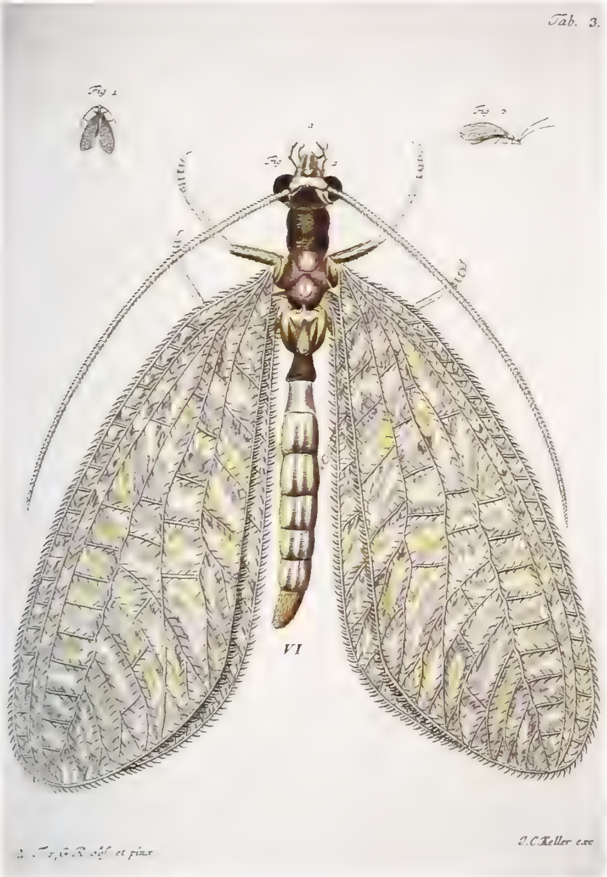


Abb. 8: W. F. VON GLEICHEN (1764b), Tafel zu der Arbeit über „Die Hofdame“ (= *Chrysoperla carnea*).

VON GLEICHEN mutmaßte, dass seine „Hofdame“ „die nemliche ist, welche nach der Beschreibung des Herrn von RÉAUMURS aus der seidenartigen Puppe hervorkomt“. Das ist sicher nicht richtig, aufgrund der biologischen Angaben von RÉAUMUR kann es sich nicht um eine *Chrysoperla*-Art gehandelt haben. Auch VON GLEICHENS Vermutung, dass seine „Hofdame“ sich aus einem „entkommenen Blatlausfreßer“, der im „Zimmer eine ... anständige Speise“ gefunden habe, entwickelt habe und „dass durch die Wärme geheizter Zimmer, wie dies bei allen sich verwandelnden Insekten geschieht, das Wachstum und Auskriechen der Fliege dergestalt befördert worden ist, daß letzteres im Jenner erfolget, da es nach Herrn von RÉAUMUR bei den Spätlingen erst im Frühjahr geschieht..“ trifft natürlich nicht zu. RÉAUMUR hat über eine Spezies geschrieben, die nicht als Imago überwintert.

Erstaunlich ist indes, dass VON GLEICHEN offenbar erst kurz vor der Veröffentlichung seines Artikels über die „Hofdame“ (er war damals immerhin schon 47 Jahre alt) eine Florfliege beachtet hat, denn nichts in den beiden Artikeln, die sich mit Chrysopiden befassen, deutet darauf hin, dass VON GLEICHEN diese Insekten vorher gekannt hatte. Kaum ein an der Natur und insbesondere an Insekten interessierter Mensch in Mitteleuropa begegnet nicht schon früh, meist irgendwann in der Kindheit, einer Florfliege und erkennt die charakteristischen, in etwa 30 Arten in Mitteleuropa vorkommenden Neuropteren immer wieder. Auch und besonders an den bräunlich verfärbten Florfliegen kann man im Spätherbst, Winter oder Vorfrühling kaum vorübergehen, weil sie in fast allen Häusern, die von Gärten oder gar Feldern umgeben sind, vorkommen; oft findet man sie – besonders in alten Häusern – zwischen Fenstern, wo sie manchmal in Ritzen überwintern.

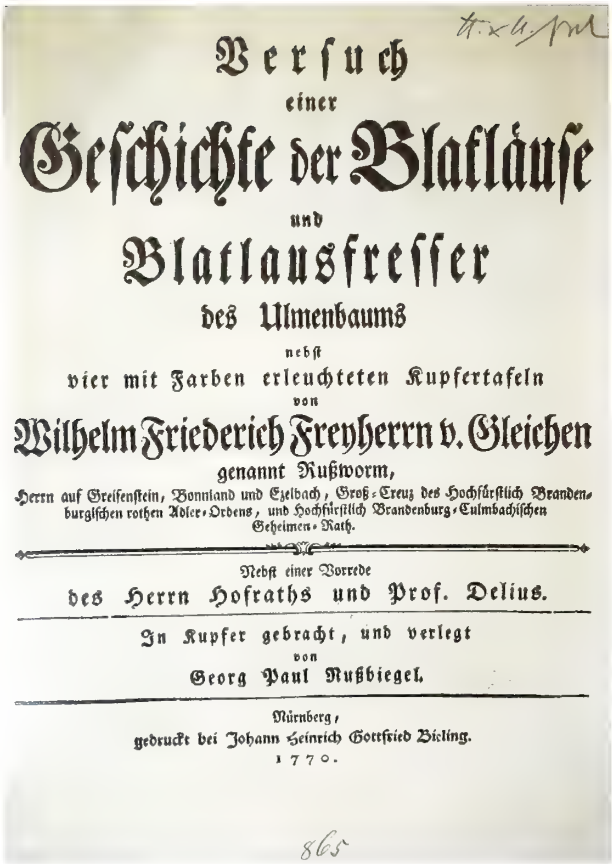
In allen größeren entomologischen Werken, die vor 1764 existierten, sind auch Chrysopiden behandelt und auch abgebildet worden.

Bei aller Würdigung der Verdienste VON GLEICHENS erstaunt es doch, dass ein in einer so sorgenfreien materiellen Situation lebender Mensch mit einer so ausgeprägten Neugierde für die Natur nicht über die entomologischen Standard-Werke, die im 17. und 18. Jahrhundert erschienen waren, verfügte. Er muss demnach zumindest in den ersten Jahren seiner naturwissenschaftlichen Studien auf Schloss Greiffenstein nur eine bescheidene Bibliothek besessen haben.

4. 1770: „VERSUCH EINER GESCHICHTE DER BLATLÄUSE UND BLATLAUSFRESSER DES ULMENBAUMS“ (ABB. 9-12)

Diese 1770 und in einer 2. Auflage 1787 erschienene, insgesamt 30 Seiten umfassende und mit vier kolorierten Kupferstichen ausgestattete Publikation zählt zu den bekanntesten Arbeiten des Autors und ist zumindest von MORTON (1910), WEIDNER (1980), GEUS (1989) und DETTNER (1997) besprochen worden. Im Vordergrund der Sekundärliteratur steht der Nachweis des Lebenszyklus und insbesondere der Parthenogenese der Ulmenblattlaus, *Byrsocrypta ulmi* (L.), durch VON GLEICHEN sowie dessen Überlegungen zu diesem Phänomen.

Im Zuge der Befassung mit den Blattläusen stieß VON GLEICHEN auf einen der Prädatoren unter den Neuropteren, jene charakteristische Hemerobiiden-Spezies, die LINNAEUS (1758) als *Hemerobius phalaenoides* beschrieben hat und die später in das Genus *Drepanepteryx* Leach transferiert wurde.



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Verſuch
einer
Geſchichte der Blatläuſe
und
Blatlausfreſſer
des Ulmenbaums
nebſt
vier mit Farben erleuchteten Kupfertafeln
von
Wilhelm Friederich Freyherrn v. Gleichen
genannt Rußworm,
Herrn auf Greifenſtein, Bonnland und Ezelbach, Groß-Creuz des Hochfürſtlich Brandenburgiſchen rothen Adler-Ordens, und Hochfürſtlich Brandenburg-Culmbachiſchen Geheimen-Rath.

Nebſt einer Vorrede
des Herrn Hofraths und Prof. Delius.

In Kupfer gebracht, und verlegt
von
Georg Paul Nußbiegel.

Nürnberg,
gedruckt bei Johann Heinrich Gottfried Bieling.
1770.

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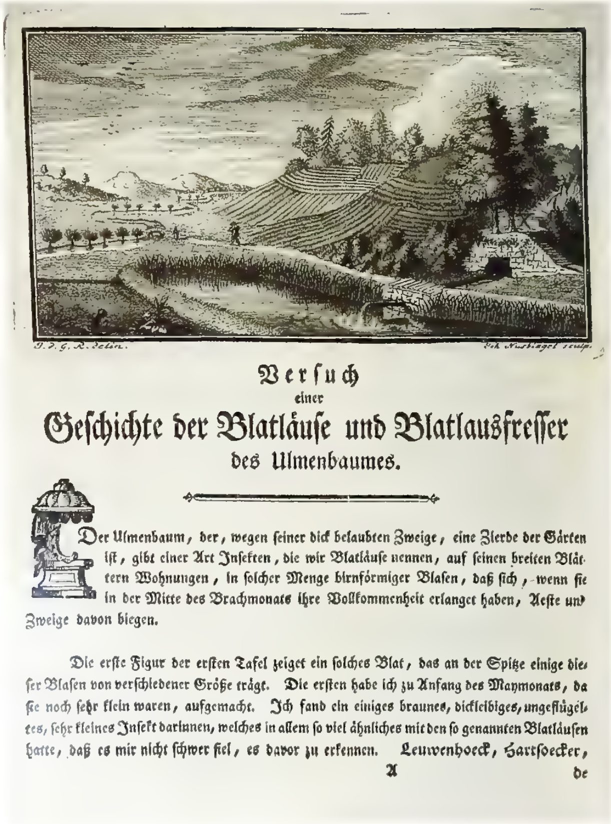
Abb. 9: W. F. von Gleichen (1770), Titelblatt (Bibl. H.& U. Aspöck)



J. d. G. R. delin. Joh. Nusbiegel sculp.

Verſuch
einer
Geſchichte der Blatläuſe und Blatlausfreſſer
des Ulmenbaumes.

Der Ulmenbaum, der, wegen ſeiner dick belaubten Zweige, eine Zierde der Gärten iſt, gibt einer Art Inſekten, die wir Blatläuſe nennen, auf ſeinen breiten Blättern Wohnungen, in ſolcher Menge birnförmiger Blaſen, daß ſich, wenn ſie in der Mitte des Brachmonats ihre Vollkommenheit erlanget haben, Aeſte und Zweige davon biegen.

Die erſte Figur der erſten Tafel zeiget ein ſolches Blat, das an der Spitze einige dieſer Blaſen von verſchiedener Größe trägt. Die erſten habe ich zu Anfang des Maymonats, da ſie noch ſehr klein waren, aufgemacht. Ich fand ein einiges braunes, dickleibiges, ungeflügeltes, ſehr kleines Inſekt darinnen, welches in allem ſo viel ähnliches mit den ſo genannten Blatläuſen hatte, daß es mir nicht ſchwer fiel, es davor zu erkennen. Leuwenhoeck, Hartſoecker,

A de

Abb. 10: W. F. von Gleichen (1770), erste Seite (mit der von „J.d.G.R." [= J. von Gleichen-Russworm? Ein Verwandter?] gezeichneten und von Johann Nusbiegel (1750-1833) gestochenen Vignette.

Etwa sieben Seiten Text und zwei kolorierte Kupferstiche widmet von Gleichen der Beschreibung der Larve und der Imago von *D. phalaenoid*es (Abb. 10 - 12). Die Zeichnungen hat von Gleichen – wie in seinen Werken durchwegs – selbst angefertigt, die Tafeln wurden von seinem Verleger, dem Kupferstecher Georg Paul Nußbiegel (um 1713 – 1786), gestochen.

Von Gleichen beschreibt, wie er in dem Gewimmel der jungen Blattläuse "einige braune Würmer" erblickt habe, „die sehr ämsig waren, und ihre 6. langen Beine mit ungemeiner Geschwindigkeit zu gebrauchen wusten". Er hielt „sie sogleich für das, was sie waren, nemlich für diejenige Art Blatlausfreßer, die bei dem Herrn von Réaumur die zwote Claße machen, und welchen er den Nahmen Blatlaus-Löwen, Lion de Pucerons, gegeben hat", womit von Gleichen recht hatte. Er beschreibt die Larve von *D. phalaenoides* sehr genau und gibt eine gelungene Abbildung (Abb.11: Tab. III, Fig. 21-22). Erwähnung verdient auch seine Bemerkung über den Geruch der Larven, er sei „außerordentlich stark, und dabei sehr angenehm, nichts anders als Quändel und Thimian. Vielleicht ist er die Witterung der Blatläuse die sie locket, ihrem Feinde in der Nähe zu bleiben." Tatsächlich haben die Larven von *D. phalaenoides* einen charakteristischen Geruch, den Fulmek (1941) mit dem von Anis- oder Fenchelöl vergleicht. Von Gleichen beschreibt das Verhalten der Larven sehr treffend und widmet sich dann recht ausführlich den Mundwerkzeugen. Er lobt auch an dieser Stelle zunächst die Arbeiten von Réaumur, schreibt aber dann, dass er – Réaumur – „gleichwohl bei der Untersuchung erstgedachter Kopfteile des Blausfreßers [sic!], ohnfehlbar aus Mangel recht brauchbarer Vergrößerungswerkzeuge, dießmal von seiner gewöhnlichen Bahn abgekommen" sei. Und weiter meint er, er habe daher „viel vergebliche Zeit und Mühe angewendet, auch hier [seine] Beobachtungen" mit jenen von Réaumur „zu vereinigen, ohne die Oefnungen an den Spitzen der Fresszangen des Blatlausfreßers zu finden". Darauf zitiert er Réaumur im Original, der völlig richtig Bau und Funktion der Saugzangen beschreibt. Merkwürdig, dass von Gleichen bei der Beschreibung der Mundwerkzeuge von *Drepanepteryx phalaenoides* nicht auf seine 1764 veröffentlichte Untersuchung über den „Blatlausfreßer ... an einem Hanflblat" und auf das Bezug nimmt, was er dort über Réaumurs Meinung über die „Fresszangen" gesagt hat, nämlich, dass sie nicht zum Fressen,

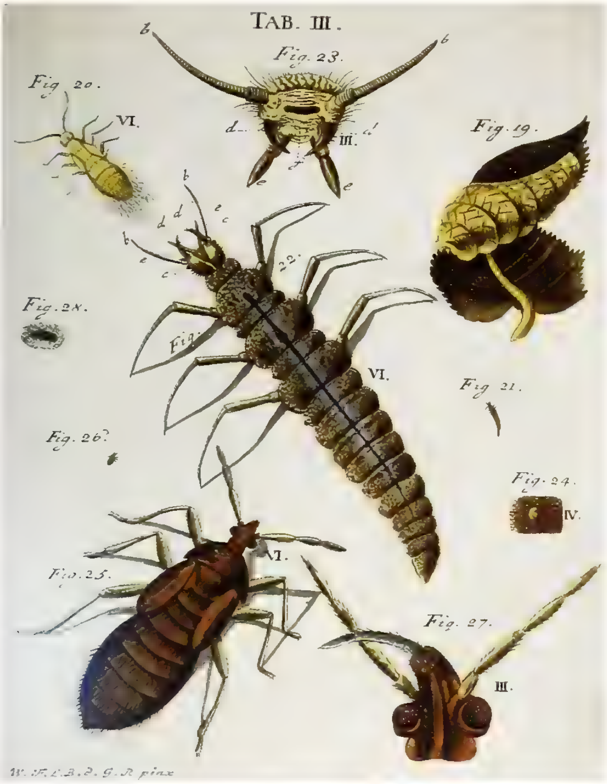

TAB. III.
Fig. 20.
VI.
Fig. 23.
III.
Fig. 19.
Fig. 28.
VI.
Fig. 21.
Fig. 24.
IV.
Fig. 25.
I.
Fig. 27.
III.

Abb. 11: W. F. VON GLEICHEN (1770), Tafel III. mit der Larve des „Ulmenblatlausfressers“ (= *Drepanepteryx phalaenoides*).

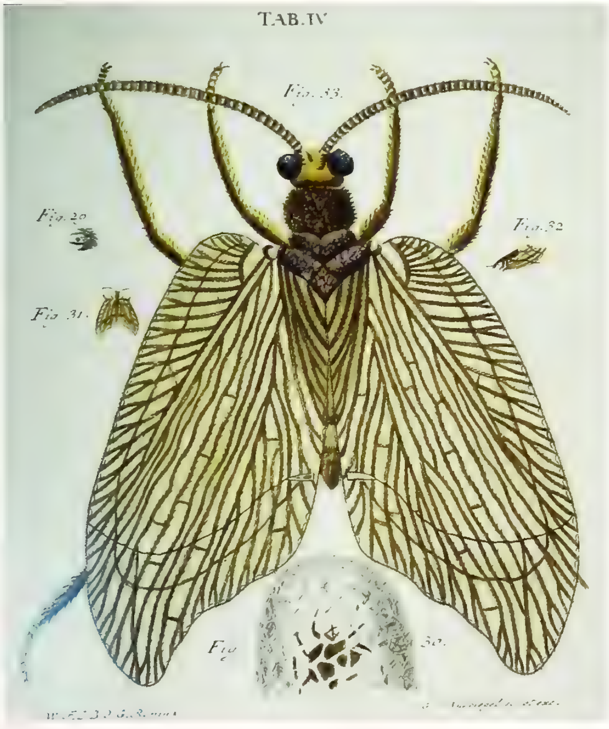
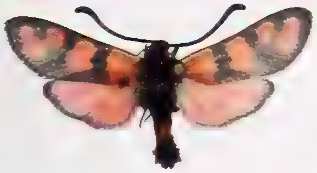

TAB. IV
Fig. 33.
Fig. 32.
Fig. 31.
Fig.
30.

Abb. 12: W. F. VON GLEICHEN (1770), Tafel IV: mit Puppenkokon (Fig. 30) und Imago (Fig. 31-33).

sondern zum Saugen dienen und „hohl und an den Spitzen offen sind“ (siehe oben). Vielmehr kam er jetzt zu dem Schluss, dass sie an den Spitzen keine Öffnungen haben, weshalb er zwischen den Saugzangen nach der Mundöffnung suchte und schließlich eine solche auch fand und sogar abbildete (Abb.11: Tab. III, Fig. 23). Dazu schreibt er: „Da aber das Maul dieses Insekts nur alleine zum Saugen, und nicht zum Nagen gebrauchet wird, so ist auch der genaue Zusammenschlus der Lippen eine natürliche Folge dieser Bestimmung, so, wie der Unmöglichkeit, solches auf andere Art, als durch einen wohl angebrachten Druck des Kopfes zu öfnen und zu sehen.“ Die akribische präparative und mikroskopische Arbeit VON GLEICHENs verdient alle Bewunderung. Die Nahrung wird bei allen Neuropteren-Larven über die Saugzangen aufgenommen, die Mundöffnung ist eine zwischen den Saugzangen quer verlaufende, falzartig verschlossene, kaum erkennbare Spalte ohne jede Funktion für die Nahrungsaufnahme. Wie hat sich VON GLEICHEN die Nahrungsaufnahme wohl wirklich vorgestellt, da er meinte, das die „Fresszangen“ keine Öffnung haben, das Maul aber zum Saugen dient. Es ist tatsächlich erstaunlich, mit welcher Bestimmtheit VON GLEICHEN die richtige Deutung der Saugzangen durch RÉAUMUR verwirft und durch eine durchaus falsche und unlogische Behauptung ersetzt.

Dann beschreibt VON GLEICHEN die Entwicklung von *D. phalanoides*, gibt die Larvalperiode mit 13 bis 14 Tagen an, erwähnt den „Bemerkungswürdige[n] Umstand, bey diesem Insekt, daß es dieses mit den Spinnen gemein hat, aus dem Ende oder der Spize seines Leibes, und nicht, wie andere Insekten aus dem Munde zu spinnen, und zwar nur zu der Zeit, wenn man das Gespinnste zu seiner Verwandlung anfängt, ohne zuvor jemals nur das geringste Merkmal, daß er hiezu geschickt sey, gegeben zu haben.“ VON GLEICHEN gibt eine schöne Abbildung des Kokons (Abb. 12: Tab. IV, Fig. 30) und erwähnt dann, dass zwei Imagines geschlüpft seien. Es folgt eine ausführliche und anschauliche Beschreibung der Imago, ergänzt durch die schöne kolorierte Kupfertafel. Gerechterweise muss man aber sagen, dass die Art zwar sofort zu erkennen ist (nicht zuletzt, weil es in Europa keine andere nur halbwegs ähnliche Hemerobiiden-Spezies gibt und die zweite in Europa vorkommende Art des Genus, *D. algidus* (Erichson in Middendorf, 1851), sich habituell erheblich unterscheidet), dass aber das Geäder recht fehlerhaft gezeichnet ist. Auch hier gilt das bei VON GLEICHENs Abhandlung über die „Hofdame“ Gesagte. Im 18. Jahrhundert unterschätzte man einfach die Gesetzmäßigkeiten des Flügelgeäders von Insekten erheblich und achtete bei bildlichen Wiedergaben vielmehr darauf, den Habitus möglichst typisch zu erfassen – was VON GLEICHEN ja auch recht gut gelungen ist.

RÉAUMUR (1737) hat die Larve, den Kokon mit der Puppe und die Imago des 21 Jahre später von LINNAEUS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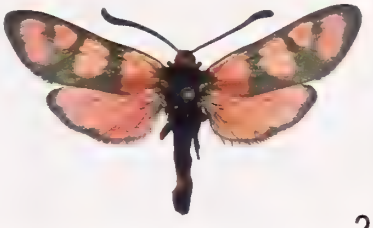
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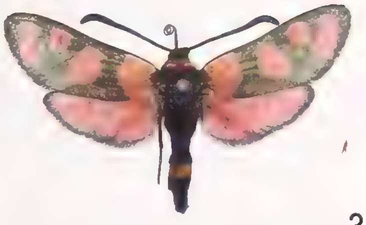
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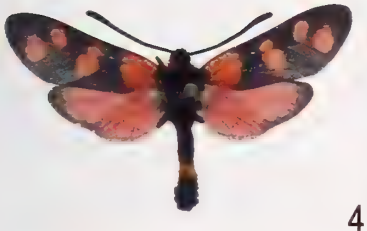
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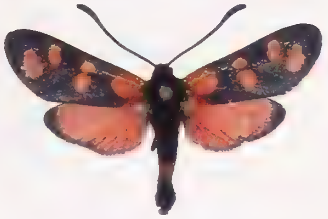
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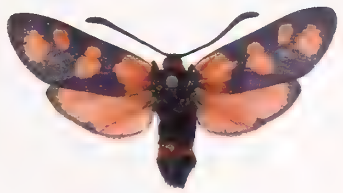
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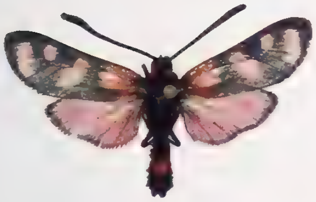
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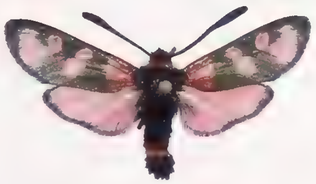
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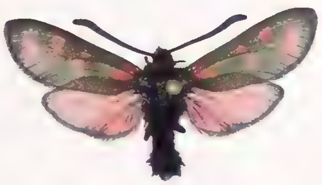
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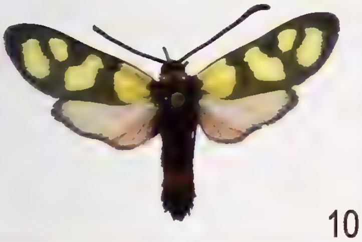
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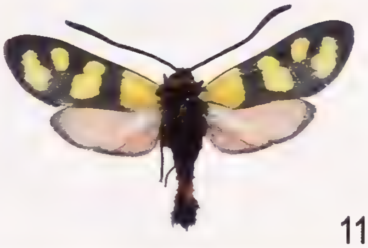
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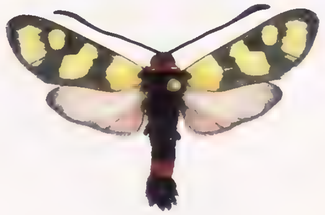
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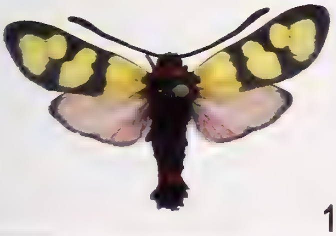
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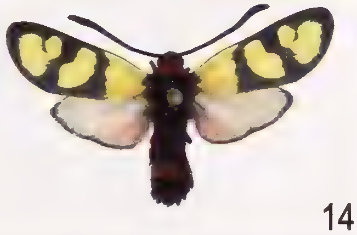
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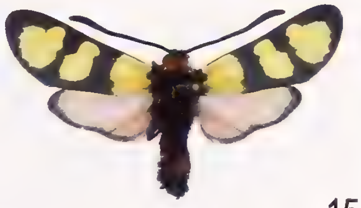
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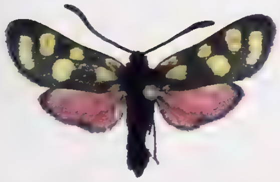
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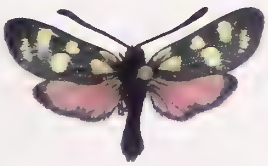
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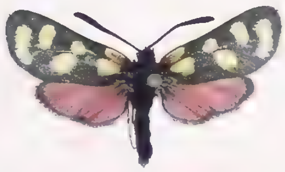
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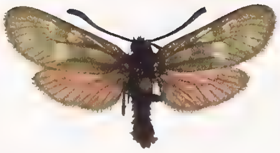
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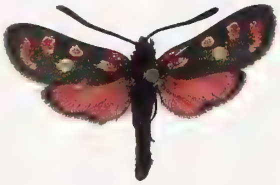
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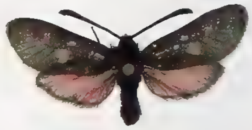
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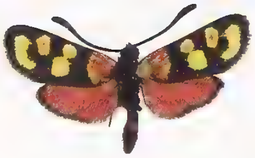
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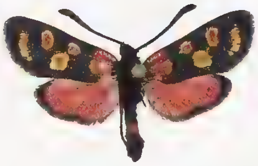
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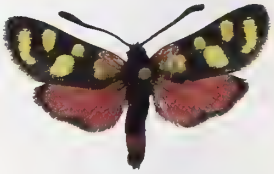
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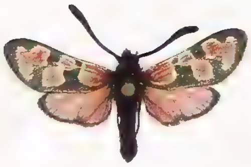
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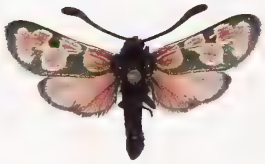
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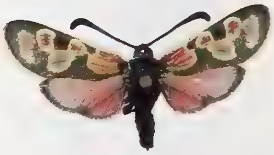
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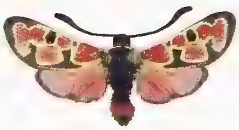
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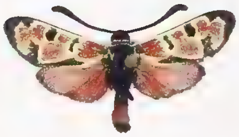
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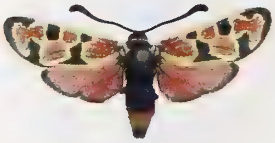
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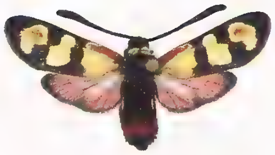
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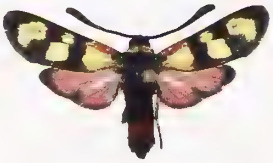
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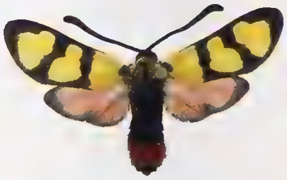
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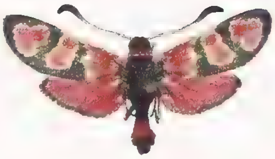
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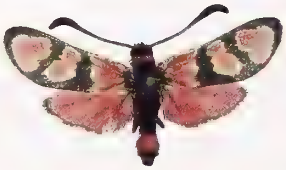
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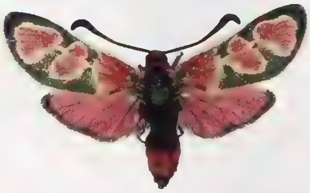
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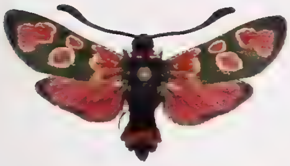
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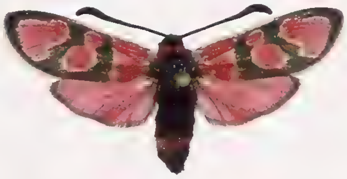
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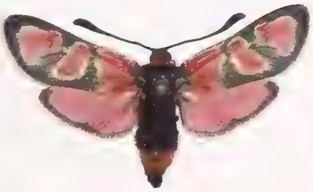
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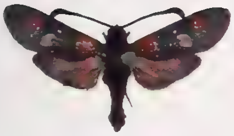
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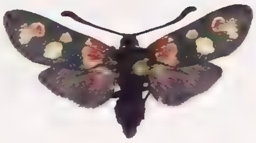
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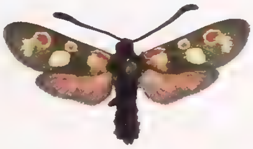
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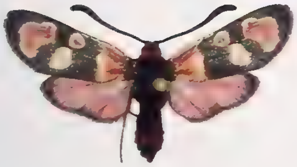
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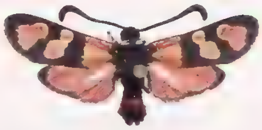
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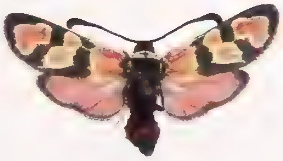
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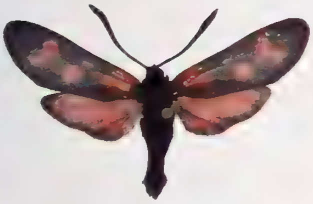
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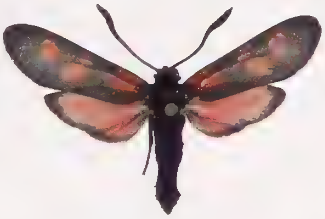
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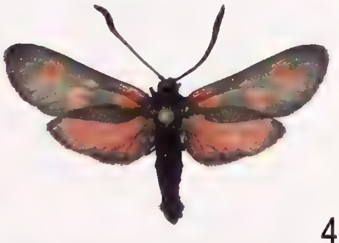
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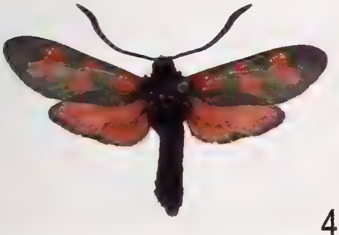
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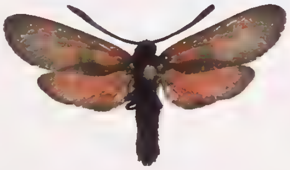
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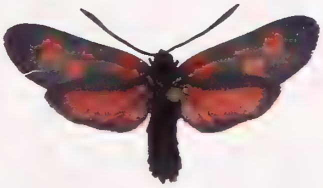
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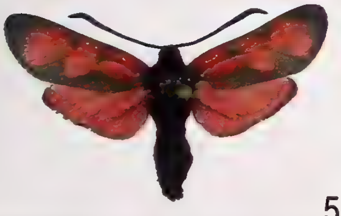
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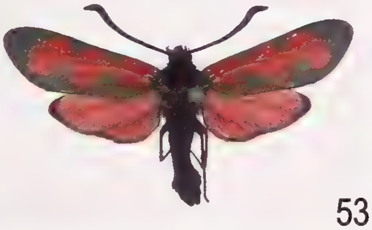
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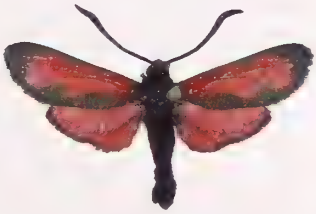
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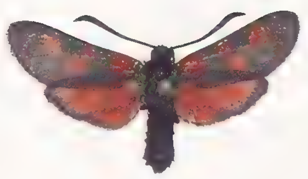
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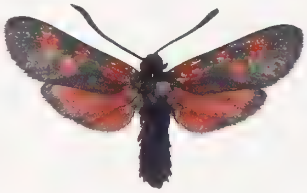
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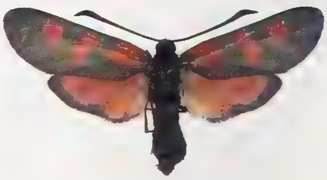
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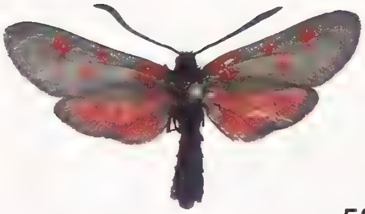
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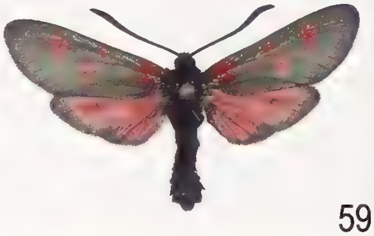
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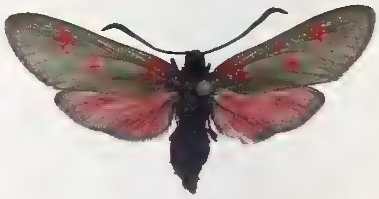
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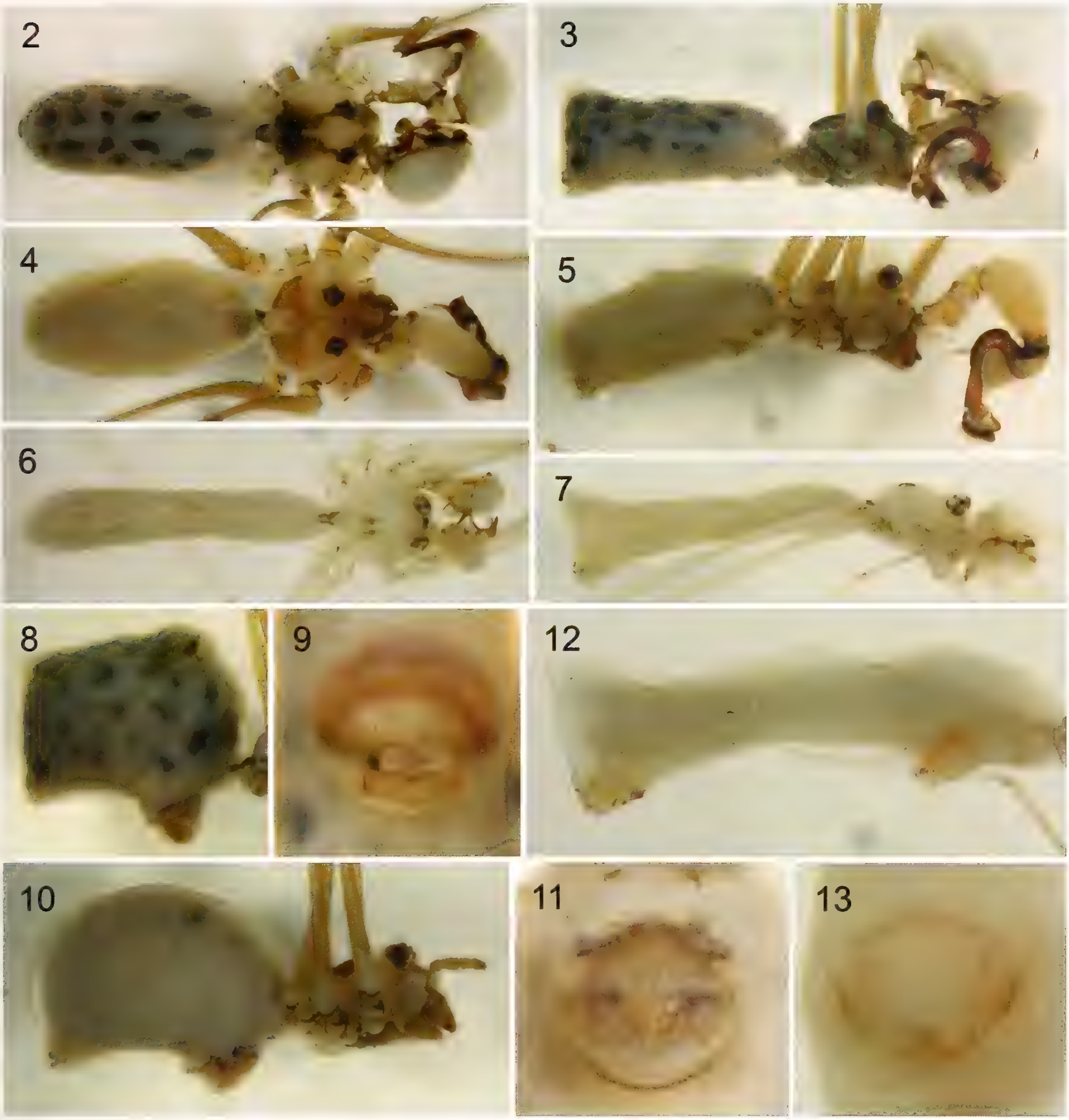

Figs. 2-13: Habitus and female external genitalia photographs. 2-3. *L. brazlandia*. 4-5. *L. pataxo*. 6-7. *L. evaluna*. 8-9. *L. brazlandia*, female abdomen, lateral view, and external genitalia, ventral view. 10-11. *L. pataxo*, female, lateral view, and external genitalia, ventral view. 12-13. *L. evaluna*, female abdomen, lateral view, and external genitalia, ventral view.

Bonner zoologische Beiträge | Band 53 (2004) | Heft 1/2 | Seiten 109–110 | Bonn, Juni 2005

First Record of *Hyles dahlii* (Geyer, 1827) (Lepidoptera: Sphingidae) from the African Mainland [1]

Anna K. HUNDSDÖRFER, Dresden

[1]The hawkmoth species *Hyles dahlii* (Geyer, 1827) is considered to be restricted to Corsica, Sardinia and the Balearic Islands (REBEL 1934), although there are occasional reports from Sicily (PITTAWAY 2004). In addition, it has also been found on the Catalan coast, in northeastern Spain, in 1975 (MASÓ PLANAS et al. 1979) and on the island of Pianosa, off the Tuscan coast (Italy) in 1998 (DAPPORTO et al. 1999).

Here I report the discovery of about 15-20 first instar (L1) larvae of *H. dahlii* feeding on *Euphorbia paralias* in northern Tunisia in October 2004. The exact locality is the beach at Residence Shiri, a small hotel and camping site on the coast north of Sejane between Cap Serrat and Bizerte. I collected and reared about a dozen individuals. After two moults it was possible to determine them as *H. dahlii* (a caterpillar is illustrated in Fig. 1 and an adult in Fig. 2). This species has to date not been reported from Africa. Voucher specimens will be deposited at the Zoologisches Forschungsinstitut und Museum Alexander Koenig (Bonn) and the Natural History Museum (London).

I doubt that *H. dahlii* is already established on the African mainland. I observed very few habitats for spurge-feeding hawkmoths in Tunisia, as I found little food plant in the parts of the country I visited. During my one-week tour (from the northern coast due south near the Algerian border, then back north along the eastern coast), I found herbaceous *Euphorbia* only along one inland stretch of road; otherwise there was only *E. paralias* along the coast. In the north, there are few sandy coastlines and these are often short and very isolated, with stretches of rocky coast and cultivated pine forest surrounding them. In parts of the eastern coast, the air is so humid that water condenses on the plants and the sand becomes baked onto them, so that they do not appear to be easily eatable by caterpillars. Also, the beaches are often partly or wholly developed for the tourist industry and thus it is possible that the populations of *E. paralias* have become relictual or destroyed due to human activities. I found no other *Hyles* caterpillars at the beach of Residence Shiri, or any indications of prior occurrence, such as droppings or nibbled plant sprouts. In contrast, on other beaches in Tunisia, and one especially on the north coast, as well as at one locality inland, I found numerous caterpillars of *H. tithymali*, but I did not find any other *H. dahlii* caterpillars. Therefore, I consider this first record of *H. dahlii* from the African mainland is probably the result of a rare dispersion event, possibly of only a single fertilised female from Sardinia, which lies geographically nearest to the Tunisian locality.

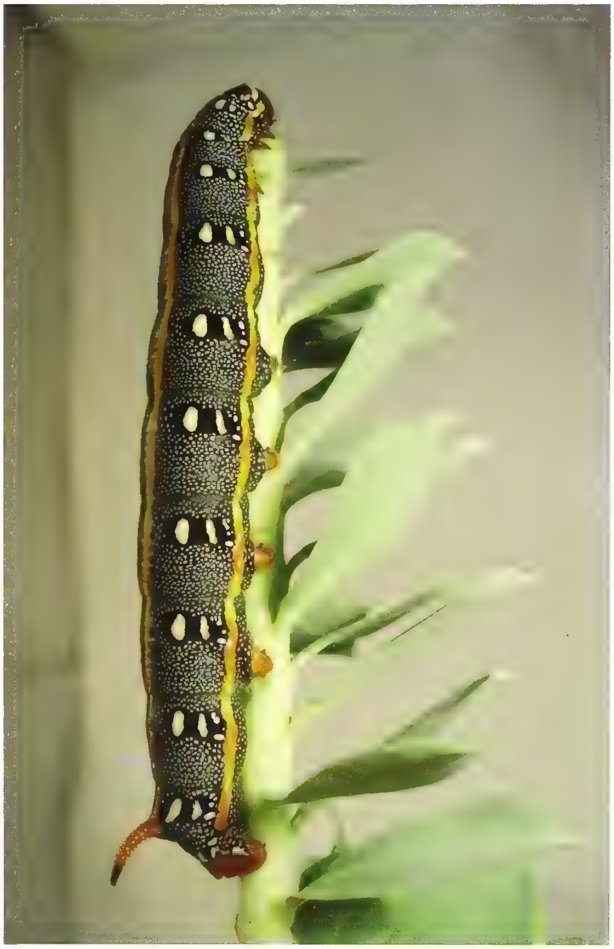

Fig. 1: Fifth instar larva of *Hyles dahlii* found on *Euphorbia paralias* in Tunisia in October 2004 (feeding in captivity on *E. myrsinites*).

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[1] Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004) zum Gedenken

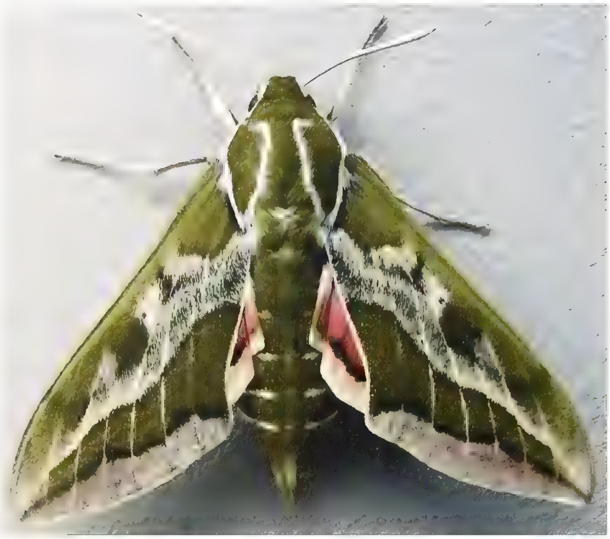

Fig. 2: An adult moth of *Hyles dahlii*, emerged from the pupa in February 2005. The individual was collected as first instar larva in Tunisia in October 2004 and reared in captivity.

Acknowledgements. I would like to thank Michael Korn (Konstanz) for this successful joint collecting trip to Tunisia and his specific help in looking out for *Euphorbia* plants and *Hyles* caterpillars. Special thanks also go to Paolo Mazzei (Rome), who first determined these larvae as *H. dahlii* on the basis of the single specimen I gave to him during my return journey. I am indebted to Ian J. Kitching (London) for his correction of my language and for very helpful suggestions to this note. I would also like to express gratitude to the late Clas Naumann for his long-term interest and participation in the collection of *Hyles* samples for our joint studies with Ian J. Kitching and Michael Wink (Heidelberg).

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tory Museum (BMNH), London, and the Museum für Naturkunde (ZMB), Berlin.

Biometric and scalation characters as well as colour pattern data were evaluated in both living and preserved specimens. Measurements were taken with a dial calipper (to the nearest mm). The following abbreviations are used: a.s.l. = above sea level, SVL = snout vent length, TL = tail length, SE = distance from snout tip to front of eye, EE = distance between hindmargin of eye to hindmargin of ear, HW = maximum head width, HH = maximum head height, HL = head length (from tip of snout to hindmargin of ear). The following scale counts were taken: supralabials (SPL), sublabials (SBL), nasals (N); in direction from rostral to labial: nasorostrals, supranasals, postnasals, internasals (IN); postmentals (PM), gulars bordering the postmentals (GP), interorbitals (IO), ventrals (V), scales around midbody (SB), subdigital lamellae under the first (LT1) and fourth toe (LT4), preanal pores (PP), postanal tubercles (PAT), dorsal scale rows in the middle of the third caudal whorl (S3R). In living specimens symmetrical scale counts were taken only on the lizard's right side. Colouration is described according to the standard plates published by GRALLERT & ROLAND (1960).

3. RESULTS

3.1. Description of *Gekko scientiadventura* sp. n.

3.1.1. Diagnosis. A small-bodied species of *Gekko*. The biggest specimen (captive) has a total length of 154 mm, of which 81 mm are made up of the tail. Habitus slender, head distinctly broader than neck, head and body slightly depressed. Unregenerated tail always longer than head-body length, not constricted at its base, not thickened, slighty depressed. Lateral fold weak, upper side of head, body and tail without tubercular scales. Digits and toes slightly webbed at the base, only interspace between toes 4 and 5 not webbed. All digits and toes, except the inner ones, clawed. 14-17 subdigital lamellae below fourth toe. 5-8 preanal pores. Nostril touches rostral. No internasals. Posterior ciliaries spiny. Upper side yellowish to brownish in life. Dorsally seven large light spots that may be expanded to lateral narrow wavy bands. Tail with 7-10 light crossbands. Gular region and parts of venter marbled.

From all species of *Gekko* known to occur in Vietnam (*G. badenii, G. chinensis, G. gecko, G. japonicus, G. palmatus, G. ulikovskii*), *G. scientiadventura* sp. n. is invariably distinguished by the lack of middorsal tubercles. For more detailed comparison, also with other *Gekko*-species see below (3.4. and 3.5.).

3.1.2. Holotype. ZFMK 76198, adult male, Figs. 1-3, primary limestone forest, Phong Nha - Ke Bang, surroundings of 17.32 N, 106.16 E, ca. 50-150 m a.s.l., Quang Binh Province, Vietnam, coll. H.-W. HERRMANN, VU NGOC THAN & T. ZIEGLER, 27-29 August 2001.

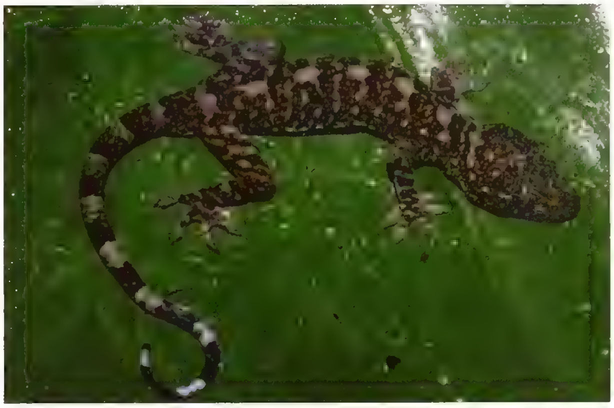


Fig. 1: Live holotype of *Gekko scientiadventura* sp. n. (ZFMK 76198). Phot. T. ZIEGLER

3.1.3. Description of the holotype. Total length 128 mm (for more measurements and indices see Table 1). Rostral twice as broad as high, narrower than mental, without a median suture. 13/12 supra- and 11/10 sublabials. Nostril touches rostral and 1st supralabial. 3/3 nasals, nasorostrals in contact medially. Nasorostrals twice as big as postnasals. Pupil vertical. Tympanum obliquely oval, ca. half of the eye diameter. Interorbital scale count 44. Mental triangular, as broad as high. Two postmentals, twice as long as broad and of subequal length with the 1st supralabial. Postmentals posteriorly touched by six scales. Lateral scales of snout about three times bigger than those on the dorsal side of the snout, roundish, juxtaposed. Head scales granular, ciliaries posteriorly spiny. Gular scales granular, about the same size as upper head scales. Dorsal scales round, smooth, juxtaposed, convex, ca. 1.5 times bigger than head scales. Ventral scales flat, smooth, imbricate, three times as big as dorsals, 41 in an oblique row between the weakly developed lateral folds. Midbody scale count 140. Scales on the upper surface of the upper fore- and hindlimbs flat, smooth and imbricate, granular on the lower. Lower parts of all limbs with granular scales. Fingers and toes basally weakly webbed, only toes 4 and 5 without webbing. 14/12 lamellae under the 1st and 17/15 under the 4th toe. 5 preanal pores arranged in an angularly bent series, 3/3 postanal tubercles. Upper caudal scales flat, subimbricate, as big as the dorsals, arranged in regular transverse rows and weakly expressed whorls, the 3rd whorl being composed of (dorsally) 10 scale rows. Subcaudals flat, smooth, imbricate, 2.5 times wider than high, with a median row of regularly arranged plates; each 3rd plate ca. 3 times as broad as high, marking the beginning of whorl. Laterally, the subcaudals are bordered by alternating scales (2-2-3-2-

2-3-2-2 ...) where scales each are bordering the respective broader subcaudal plate.

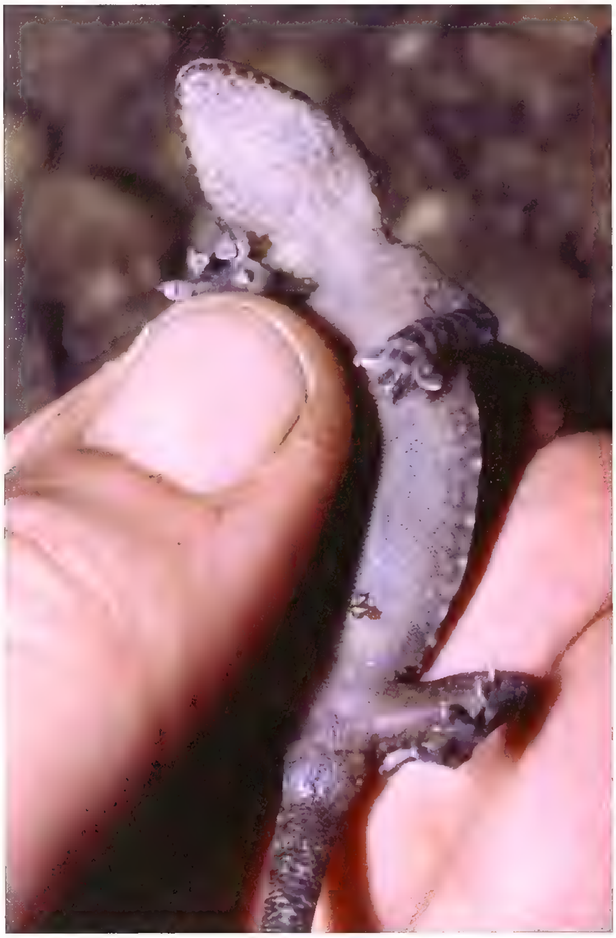


Fig. 2: Ventral view of the live holotype of *Gekko scientiadventura* sp. n. (ZFMK 76198). Phot. T. Ziegler

Hemipenial morphology. Right hemipenis (Fig. 3: terminology after Rösler 1998) 2.2 mm wide, 4.6. mm long, clavate, forked. Pedicel and truncus not differentiated from each other; basally on the sulcal side is a small wrinkled adminiculum, running laterocranially and not reaching the sperm groove. Above the adminiculum a ribbed area. Apex bilobed, the lobes being subequal in size. Sperm groove originates from the laterocaudal side of the organ and runs straight along the truncus, where it divides into two branches that terminate on the upper side of each lobe in a slit-like concavity. Apically, the sperm groove is shallow and is accompanied by weakly developed sulcal lips. The sperm groove gets deeper and widens towards the proximal part of the truncus. The epidermal tissue of the lobes appears to be rough, although no calyces can be distinguished.

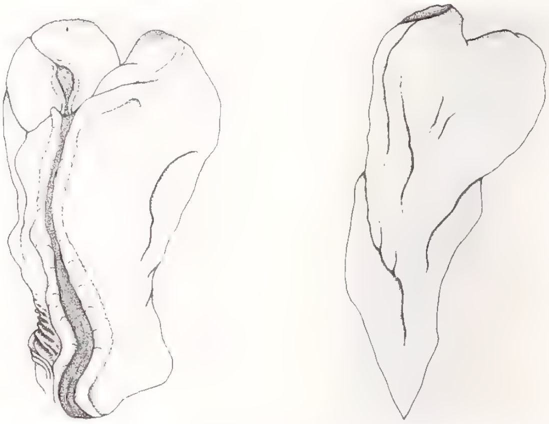


Fig. 3: Right hemipenis of the holotype of *Gekko scientiadventura* sp. n. (ZFMK 76198): a) sulcal, b) asulcal view. Drawing: H. Rösler.

Colour of preserved holotype. Upper side of head and body dark grey. Head grey-brown, with darker vermiculations and flecks, additionally small light dots. Dorsum with seven median light flecks that continue laterally into small transverse bands with strongly waved anterior and posterior margins. These transverse bands are anteriorly bordered by brown-blackish lines and dissolve laterally. Between the single bands light flecks and numerous small spots are interspersed. Limbs above dark grey with grey-brown stripes. Throat, chest and belly buff, the throat bearing a reticulate pattern. Belly laterally with light spots. Forepart of tail above and below dark grey, hindpart grey-black. Nine grey-brown transverse bands on the upper side of tail, the hindmost five reaching the lower side of the tail and nearly form closed rings.

3.1.4. Paratypes. ZFMK 76174 (Fig. 4), adult female, ZFMK 76175-179, juveniles, Phong Nha - Ke Bang, surroundings of 17.32 N, 106.16 E, 50-150 m a.s.l., Quang Binh Province, Vietnam, coll. H.-W. Herrmann, Vu Ngoc Thanh & T. Ziegler, 26 August - 1 September 2001. ZFMK 80651-652, adult females, same locality data, coll. Vu Ngoc Thanh & T. Ziegler, 29 August - 10 September 2003.

Paratypes ZFMK 76179 and 80652 will be permanently transferred to the scientific collection of the Vietnamese National University, Hanoi (HNUV).

3.1.5. Description of paratypes. Individual body measurements and proportions can be seen in Table 1. For the latter, the paratypes have the following mean values and standard deviations (n being variable): SVL:TL 0.87+/-0.07, SVL:HL 3.49+/-0.24, HL:HW 1.28+/-0.03, HL:HH 2.28+/-0.03, SE:EE 1.33+/-0.09.

All paratypes possess invariably 3 nasals, no internasals and 2 postmentals. Further, females and juveniles are lacking preanal pores. The postmentals are differently shaped, the maximal relative length is the left postmental of ZFMK 76176 which is three times as long as

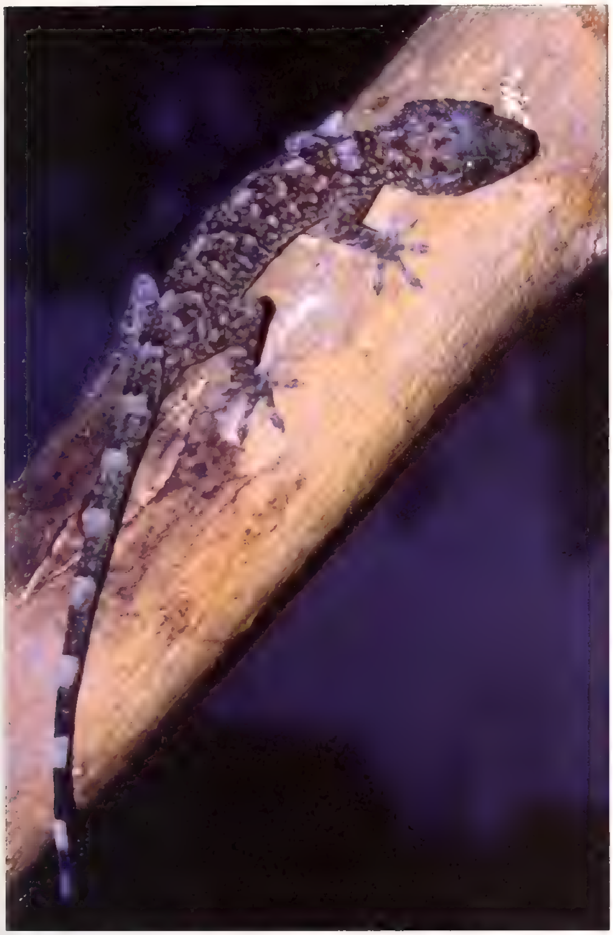


Fig. 4: Live female paratype of *Gekko scientiadventura* sp. n. (ZFMK 76174). Phot. T. ZIEGLER

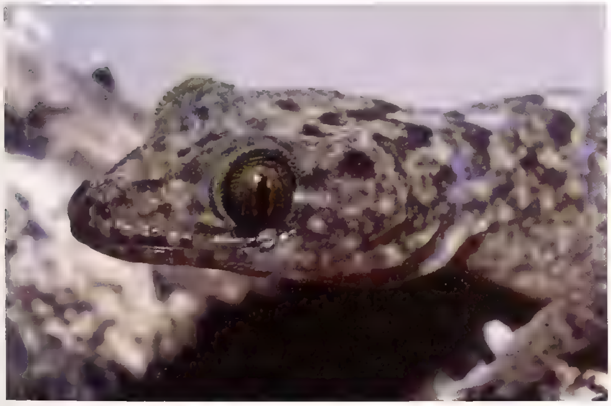


Fig. 5: Portrait of one of the captive males of *Gekko scientiadventura* sp. n. (see also fig. 28 in ZIEGLER et al. 2004) from 22 April 2003, measuring a SVL of 67 mm and a TL of 70 mm at the time; note the spiny posterior ciliaries as well as the bordering nasorostrals. Phot. T. ZIEGLER

broad. The right postmental is divided in ZFMK 76176 and 76178. The posterior ciliaries are spiny in all paratypes. The remaining scalation characters vary to a small degree only (see Table 2). Range (mean and standard deviation) of the number of supralabials is 12-14 (13.00+/-0.82), of the sublabials 9-13 (9.94+/-1.26), of the scales behind postmentals 5-7 (5.67+/-0.71), of the interorbitals 41-49 (43.75+/-3.59), of the ventrals 38-48 (41.80+/-3.90), of the scales around midbody 118-139 (132.20+/-8.23), of the lamellae under the 1st toe 12-15 (13.86+/-1.03), of the lamellae under 4th toe 14-17 (15.64+/-1.15), of the postanal tubercles 2-3 (2.50+/-0.53) and of the number of dorsal scales in the 3rd tail whorl 10-11 (10.29+/-0.49).

All juvenile paratypes (as well as two embryos, see 3.1.6.) have still two egg teeth which touch each other apically as it is typical for geckos with relative thick and calcified eggshells (RÖSLER 2001b). The tooth crown of the egg teeth has a shape similar to that of *G. gecko* (see SLUITER 1893).

Colour of preserved paratypes. The pattern of the preserved material corresponds to that of the living animals, the overall colouration being more greyish.

3.1.6. Other material. Next to the type series, there are two male embryos (ZFMK 76199 and CPHR 2028) and three eggshells (ZFMK 76180) from the same locality. The embryonic males exibit egg teeth as decribed above, their hemipenes are completely everted, deeply forked and show two subequal apical lobes. In one of them (CPHR 8028) the dark pigments (6 crossbands) start to develop.

In addition there are three males and one female (Figs. 5-7, see also fig. 28 in ZIEGLER et al. 2004) that had hatched in September/October 2001 from eggs found in a karst cave at the type locality in August 2001, and which are kept alive in the Cologne Zoo.

3.1.7. Colouration in life. Variable in all adults. Basic colour either more brownish marbled with yellowish flecks, or yellowish with brownish marbling. Upper side of head with large, blackish-brown flecks or spots which may be present also on the snout. Some specimens additionally possess some greyish flecks on the same head regions. Ciliary scales black with yellow margins. Iris metallic green-yellowish, pupil with bronze-coloured margin. A row of 7 middorsal grey flecks which may be extended to wavy crossbands of the same colour towards the flanks. These crossbands may be dissolved into flecks. The middorsal flecks are anteriorly bordered with a blackish brown pattern that is w-shaped in the neck region. The grey crossbars on the tail are likewise anteriorly bordered by blackish brown pattern elements. The grey flecks on the limbs are bigger on the hind legs. Throat and belly with more or less distinct lemon to buff colouration, with more or less distinct brown-olive marbling. Colour pattern of underside of tail variable, with pale or dark grey to ochre or blackish brown flecks.

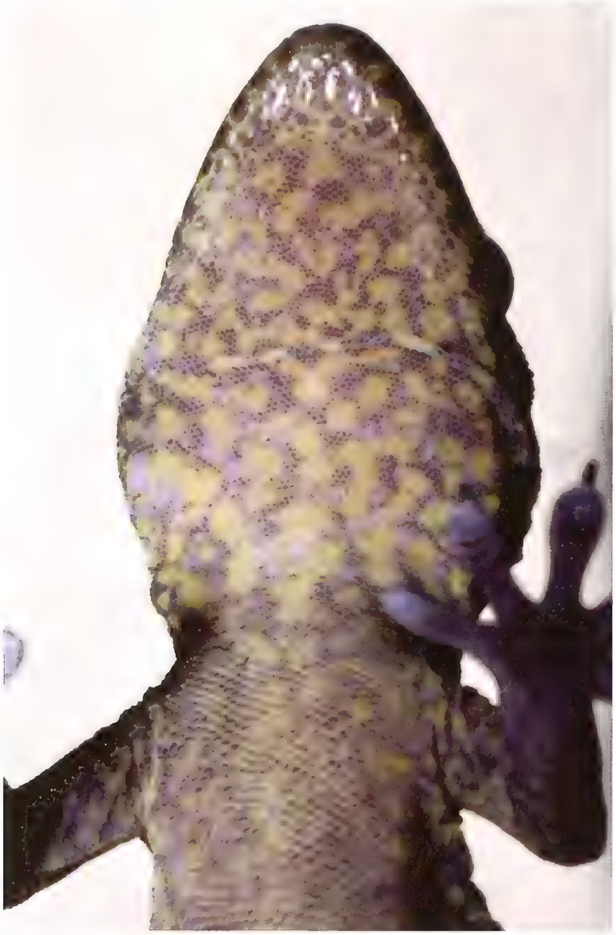


Fig. 6: Gular region of the male of *Gekko scientiadventura* sp. n. depicted in Fig. 5 (10 November 2003). Phot. T. ZIEGLER

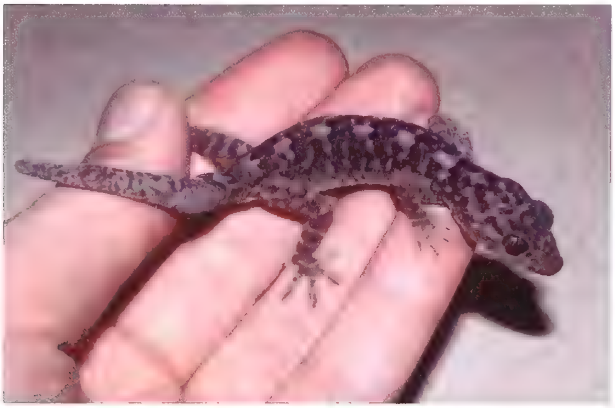


Fig. 7: Captive female of *Gekko scientiadventura* sp. n. (10 November 2003); note the regenerated tail. Phot. T. ZIEGLER

3.1.8. Etymology. The species name is a patronym for a scientific magazine programme of the German Television channel ZDF called "Abenteuer Wissen" (adventure of knowledge) in order to acknowledge the first documentation of the Phong Nha - Ke Bang National Park biodiversity for the German public. First live pictures of *Gekko scientiadventura* sp. n. were shown on this TV programme. The name is derived from the Latin words "scientia" (knowledge, science) and "adventura" (literally = things that will come = adventure) and is a noun in apposition.

3.2. Distribution

So far, *Gekko scientiadventura* sp. n. is known only from the type locality (Fig. 8). Although currently regarded as endemic for Vietnam, its occurrence in Laos cannot be excluded, considering the proximity of the Laotian border from the type locality.

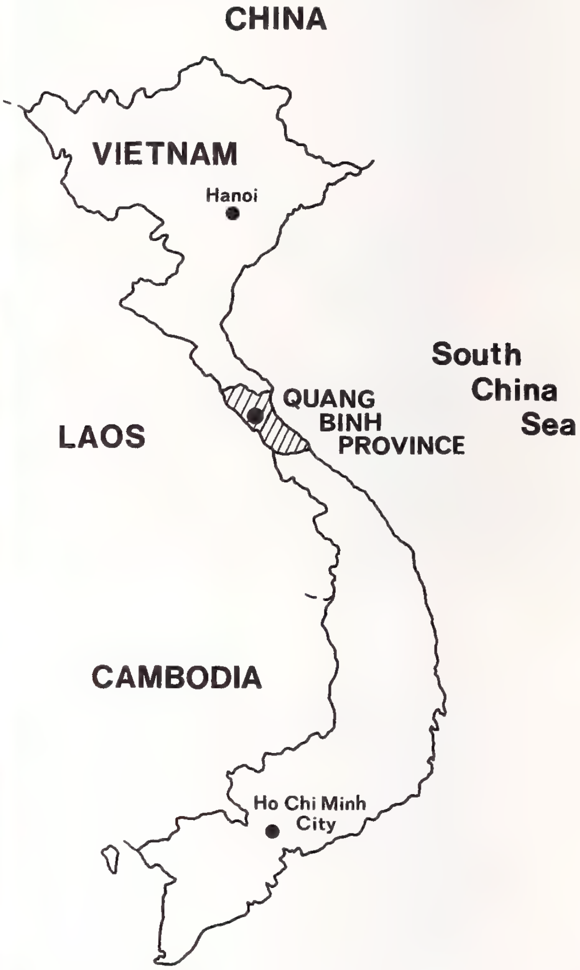


Fig. 8: Position of the type locality within Quang Binh Province.

3.3. Natural history

All specimens of the type series were collected at night in primary forest, either directly on or in the immediate neighbourhood of the karst limestone outcrops that were partly overgrown with vegetation (Fig. 9). The geckos were mostly seen on the vegetation in low height (1.0-2.5 m) rather than on the bare rocks. In contrast, these bare rocks were mostly populated by the syntopic and only recently described bent-toed gecko *Cyrtodactylus phongnhakebangensis* which, in turn, tended to avoid the vegetational parts of the microhabitat (ZIEGLER et al. 2002).

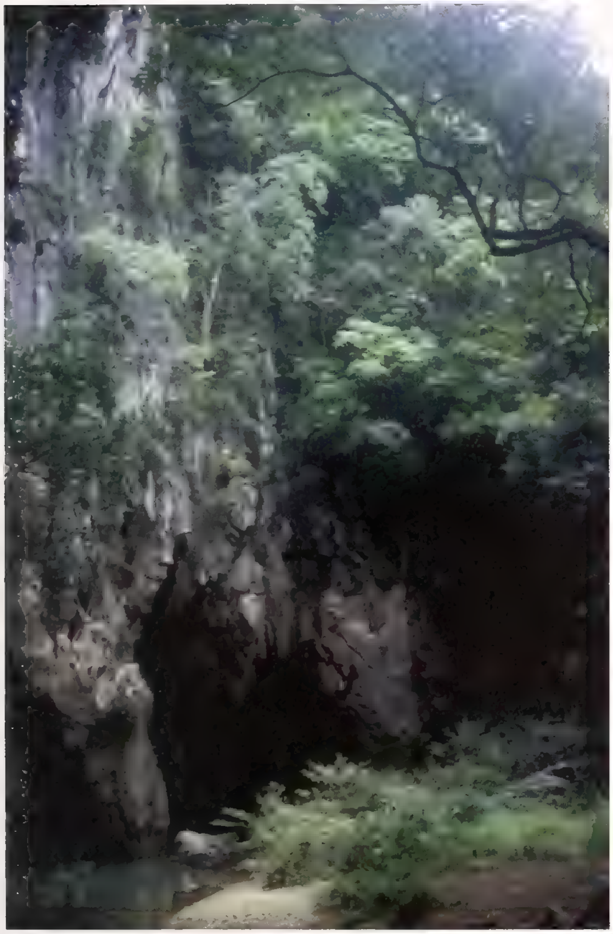


Fig. 9: Habitat of *Gekko scientiadventura* sp. n. near the type locality. Phot. T. ZIEGLER

Apart from the voucher material of our type series no further sightings of *Gekko scientiadventura* sp. n. were made, with the exception of a mass egg-laying site in a dark, manifold rock crevice system at the type locality. Fig. 10 shows this site (in about 2.5 m height) at the beginning of the rainy season (end of August) in 2001. The four geckos cited under "Other material" originate from these eggs; they hatched in September/October 2001 which correlated with the beginning rains. One year later, in August 2003, we found two glued eggs just at this mass egg-laying site. In addition, two further communal egg-laying places were found in this cave system which seemed to be used also already since a longer period; they contained, however, much less eggs and were situated much higher (ca. 5 m high).

On August 30, 2003, we measured at the lower egg-laying site, at 14.30 h, a relative humidity of 85% and a temperature of 27.3 °C. At 21.40 h the same day the temperature was 26.3 °C and the relative humidity had increased to 93% (with a recorded minimum of 70% between 14.30 and 21.40 h). In the primary forest, outside the rock crevice system, we measured with a minimum-maximum thermometer on August 28, 2001 24.4-30.2 °C and one day later 24.3-27.8 °C. For further (long-term) climatic data from this area see HERRMANN et al. (2002).

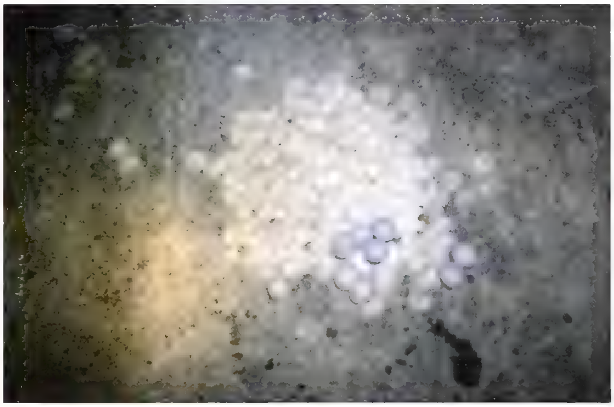


Fig. 10: Mass egg-laying site of *Gekko scientiadventura* sp. n. in a karst rock crevice at the type locality. Phot. T. ZIEGLER

One of the authors (TZ) was able to record some behavioural and autecological observations of the captive-raised geckos: The growling calls of *Gekko scientiadventura* sp. n. were mostly uttered during dawn and night, but could also be heard in summer afternoons (e.g. 22-26 July, 2002), i.e. during the light phase of the terrarium. Obviously, also the black-and-white annulation of the tail plays a role in the infraspecific communication between both sexes, because in an interacting couple the tails were raised and displayed with undulating movements. A male that was taken out of its terrarium used to wag its tail in a much faster manner. Once an acinetic reaction could be observed, a lethisimulation with a recurved tail and extremities that were raised from the ground and standing off from the body. The geckos were fed mainly with crickets of various size classes that were powdered with a vitamin-mineral mixture, however, they were repeatedly observed to lick on and even to bite off small pieces of bananas. In 2003, two egg-layings occured but the paired, partly deformed clutches proved to be unfertilised.

3.4. Comparison with other Vietnamese *Gekko* species

Next to the lack of dorsal tubercles, *Gekko scientiadventura* sp. n. can be distinguished from its Vietnamese congeners by the combination of the characters size, number of internasals and preanal pores as well as dorsal pattern:

G. badenii reaches a SVL up to 76.5 mm and has 1-3 internasals; males have 14-18 preanal pores, and the dorsal pattern consists of 4-8 very narrow and sometimes

21 subdigital lamellae under 4th toe. Males with 22-23 preanal and femoral pores; subcaudals transversely broadened (BROWN & ALCALA 1962, 1978).

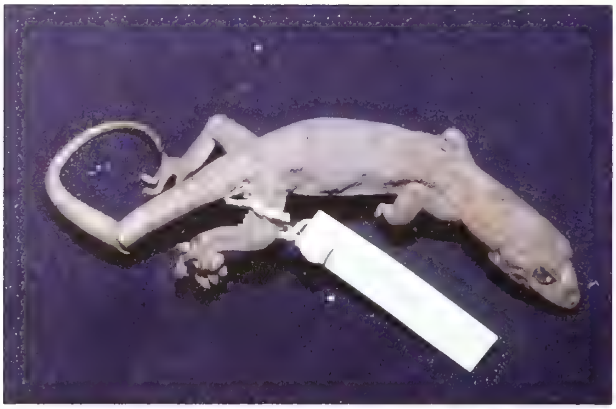


Fig. 11: Dorsal view of the holotype of *Gekko subpalmatus* (BMNH 1946.8.2592). Phot. T. ZIEGLER

G. subpalmatus reaches a SVL of 78 mm and has 1-2 internasals. Toes basally narrowly webbed. 7-10 subdigital lamellae under 4th toe. Males with 5-11 preanal pores. Subcaudals transversely broadened (GÜNTHER 1864; POPE 1935; ZHOU et al. 1989; ZHAO et al. 1999). For a better comparison with *G. scientiadventura* sp. n. we studied the holotype of *Gekko subpalmatus* (BMNH 1946.8.2592) and the lectotype and the paralectotype of *Gekko melli* Vogt, 1922 (ZMB 27659 A & B) which is considered to be synonymous with *G. subpalmatus* (e.g. ZHAO & ADLER 1993) (Figs. 11-13): The rostral of the holotype of *G. subpalmatus* has a short upper transverse suture, the posterior ciliaries are pointed, and there are five distinct tubercles anterior of the tympanum on the right side of the head. The dorsum is lilac-grey to violet-grey, a light postocular stripe and four longish grey-brown vertebral flecks are barely visible, and the tail has several broad light transverse bands that are bordered by darker pigment. The lectotype and the paralectotype of *G. melli* lack a rostral suture, the posterior ciliaries are likewise pointed, and pretympanic tubercles are lacking. The dorsum of ZMB 27659 A is olive-brown. There is a dark naso-ocular and a light postocular stripe. Two dark stripes are running from the ear openings to the axillae, and the shoulder region shows two sepia-coloured stripes. The dorsum has three broad, irregular and partly confluent, grey-brown bands with sepia-coloured margins, the tail has four broad pale brown bands that are likewise bordered by darker pigment. The regenerated tail tip has fine darker dots. Apart from their colour pattern, the types of both taxa differ also in size and in body proportions (SVL/TL index) and in the number of interorbitals, subdigital lamellae under the 4th toe, and scale rows in the third caudal whorl (see Tab. 3). Pending future studies on more material we consider *G. melli* therefore as valid.

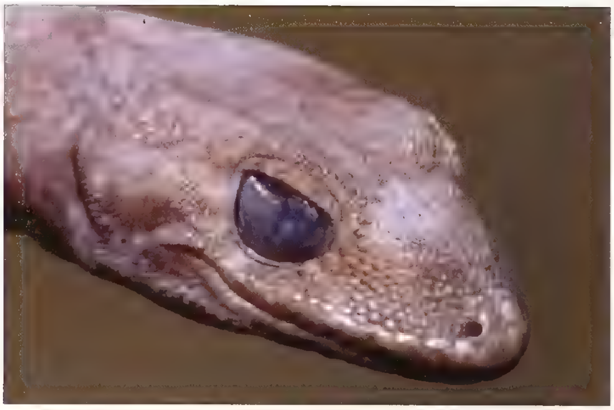


Fig. 12: Portrait of the holotype of *Gekko subpalmatus* (BMNH 1946.8.2592). Phot. T. ZIEGLER

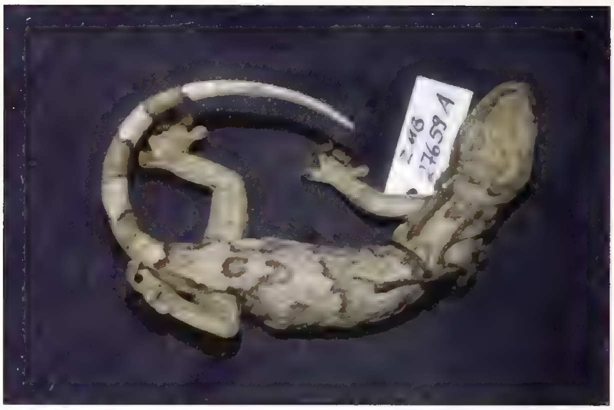


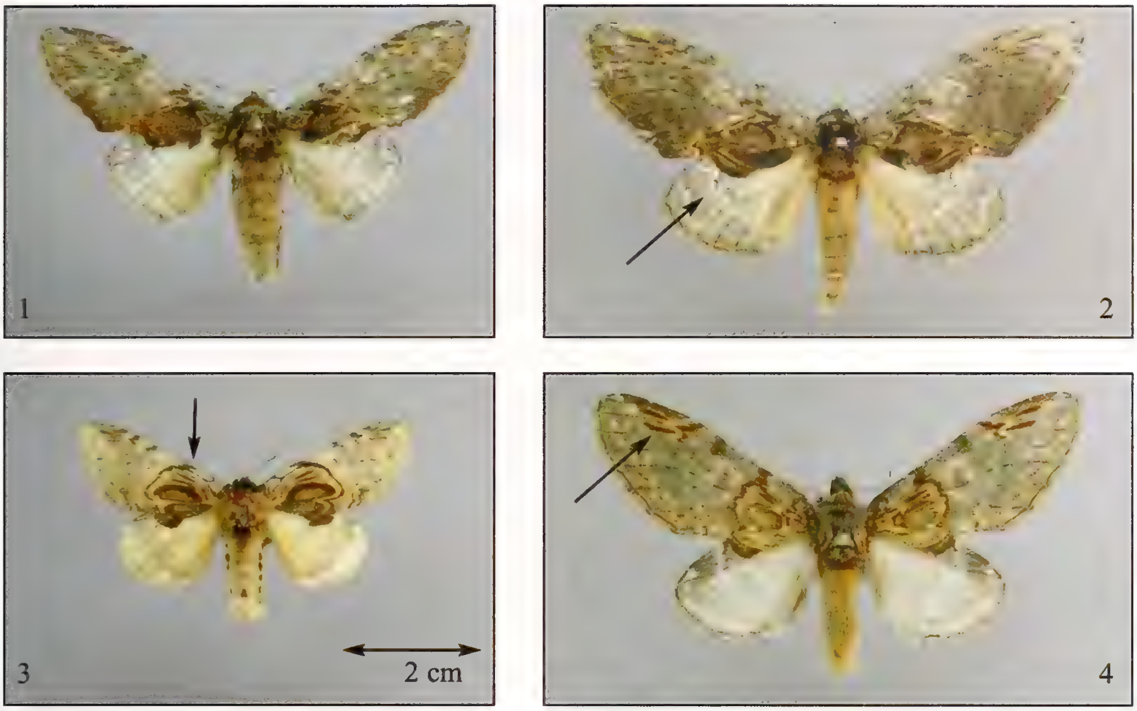
Fig. 13: Dorsal view of the lectotype of *Gekko melli* (ZMB 27659 A). Phot. H. RÖSLER

G. tawaensis reaches a SVL up to 70 mm and has internasals. The toes are basally narrowly webbed, and there are 12 subdigital lamellae under the 4th toe. The males have no preanofemoral pores, and the subcaudals are anteriorly mesially divided (OKADA 1956; SENGOKU 1989; UTSUNOMIYA et al. 1996).

G. scientiadventura sp. n. differs from the other *Gekko* species without dorsal tubercles by the combination of following characters: (a) SVL, (b) internasals, (c) extension of webbing between toes, (d) subdigital lamellae under 4th toe, (e) number of preanal pores, and (f) shape of subcaudals. *G. scientiadventura* sp. n. differs thus from *G. athymus* in the characters a, b, d, e; from *G. subpalmatus* in the characters a, b, c, d; and from *G. tawaensis* in the characters b, e, and f.

4. DISCUSSION

The genus *Gekko* Laurenti, 1768 contains, according to the last overview by KLUGE (2001) 28 species. We add to this number five more species which we consider as valid: *G. liboensis* Zhou & Li, 1982, *G. melli* Vogt, 1922, *G. mindorensis* Taylor, 1919 *G. scabridus* Liu & Zhou, 1982, and *G. scientiadventura* sp. n.



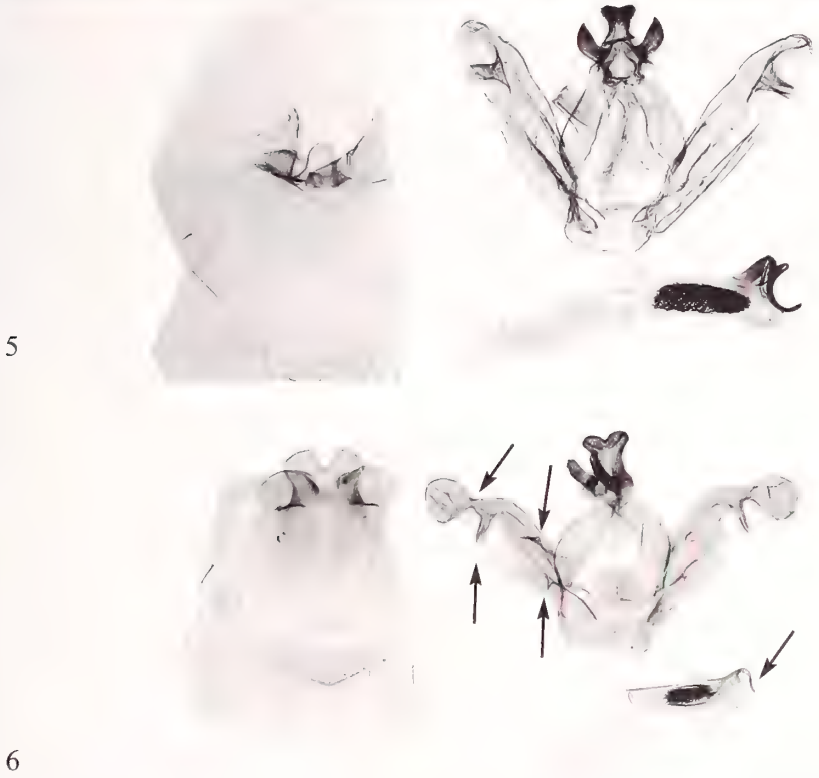
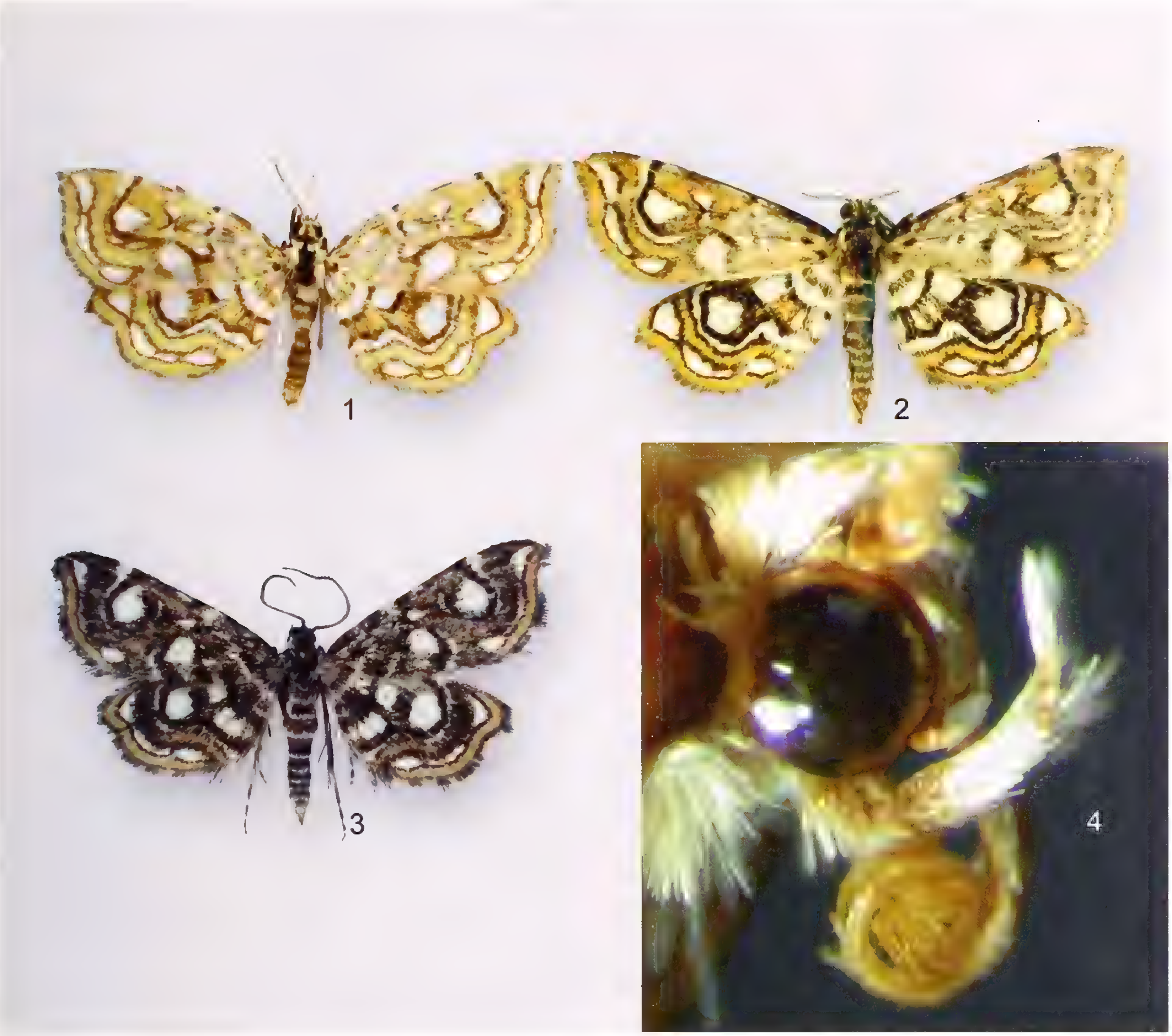


Abb. 1-4: Imagines *Peridea*. (1) *Peridea clasnaumanni* – ♂, China, NE. Jiangxi, Wuyi Shan, 1600 m, 50 km SE Yingtan, 27°56'N, 117°25'E, April 2002, Holotype. (2) *Peridea clasnaumanni* – ♀, China, Hunan, Cili, 3.ix.1988, Paratype. (3) *Peridea aliena* – ♂, Russia, Primorye, 30 km NE Wladiwostok, 24.vii.1963. (4) *Peridea hoenei* – ♀, China, Sichuan, Daxue Shan, 40 km W Mianning, 2750 m, 7.-8.vii.1998.

Abb. 5-6: Genitalapparate *Peridea*. (5) *Peridea clasnaumanni* – ♂, China, Jiangxi, Wuyi Shan, Xipaihe, 27°54'N, 117° 20'E, July 2003, 1500 m (GU 79-98), Paratype. (6) *Peridea aliena* – ♂, N. Korea, Myohang san, Myohang-Shon-valley, 24.-30.vi.1985 (GU 24-73).



Figs. 1–4:
1. *Ambia naumanni* sp. nov., holotype, male (Lijiang, 8. viii. 1934) (wing span 15 mm).
2. *Ambia naumanni* sp. nov., paratype, male (Lijiang, 13. vi. 1934) (wing span 16 mm).
3. *Ambia thyridialis* (Lederer, 1855), male (Ghazir) (wing span 15 mm).
4. *Ambia naumanni* sp. nov., male paratype, lateral view of head.

aedeagus-structure as found in *Ambia locuples* and the new species seems not advisable. We consider *Ambia thyridialis* (Lederer, 1855) (fig. 3), a species recorded from the Lebanon and Egypt which also has no saccular tooth as a closely related species.

2. DESCRIPTION OF SPECIES

***Ambia naumanni* Speidel & Stüning, sp. nov.** (Fig. 1, 2)

Holotype ♂: "Li-kiang. (China). Provinz Nord-Yuennan. 8. 8. 1934. H. Höne"

Paratypes: Males: dto. 1 ♂ 13. 6. 1934; 1 ♂ 19. 7. 1934; 1 ♂ 2. 8. 1935; 1 ♂ 17. 7. 1934; 1 ♂ 7. 8. 1934; 2 ♂ 3. 8. 1935; 1 ♂ 12. 7. 1934; 1 ♂ 7. 7. 1934, GS-15036 ♂-SB; 1 ♂ 17. 7. 1934, GU 137 ♂ SP; 1 ♂ 21. 7. 1934, Prep. 15378 SB and FU 160 SP; 27. 6. 1934, 1 ♀ 24. 6. 1935 with genitalia in glycerol;

Females: 1 ♀ 3. 8. 1935; 1 ♀ 8. 9. 1935; 2 ♀ 3. 7. 1934 with FU 159 SP; 1 ♀ 29. 6. 1934, GU 15063; 1 ♀ 15. 6. 1935; 1 ♀ "Li-kiang ca. 2000 m, Prov. Nord-Yuennan, 26. 6. 1934. H. Höne" with genitalia in glycerol.

Diagnosis (fig. 1, 2).- Head and body: Antenna comparatively stout in the males, pubescent. Labial palpi rather long, upcurved, terminal segment almost reaching base of antennae. Frons smoothly scaled, whitish like the palpi. Thorax and abdomen greyish-brown, mixed with white, abdominal tergites with posterior white tranverse bands.

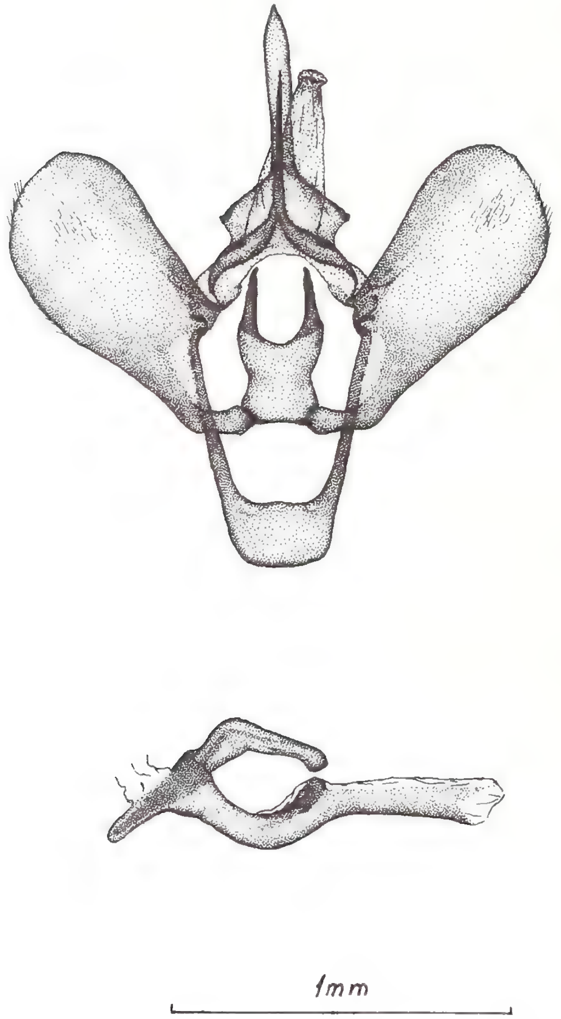


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Fig. 5: *Ambia naumanni* sp. nov., male genitalia.

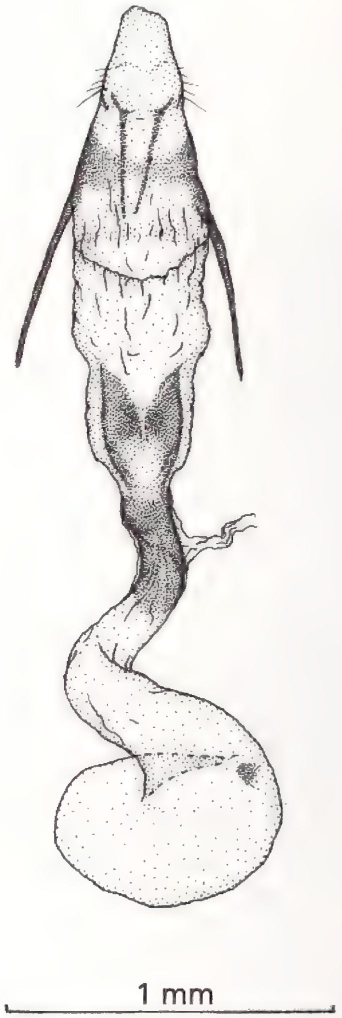

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Fig. 6: *Ambia naumanni* sp. nov., female genitalia.

Wings: Wingspan 15-17 mm, forewing length 7,5-8 mm. Wings with termen sinuous as usual in the genus, apices produced. Ground colour yellowish. Transverse fasciae prominent, white, bordered blackish-brown. The basal fascia strongly oblique, broken, the proximal one slightly curved, the distal one outcurved anteriorly and strongly retracted below middle, reaching the inner margin at about one half. The latter fascia is widened to a quadrangular spot at inner margin. Submarginal fascia conspicuous, widening towards tornus. Medial area with a white disco-cellular spot and another larger white spot in the anterior angle of the distal fascia. Marginal area yellow. Hindwing with similar pattern. Proximal fascia wider than in forewing, submarginal fascia strongly widening towards apex, incised at vein M2. Medial area suffused with brownish scales, like in the forewing, with two large white spots at the costal region and a small one at inner margin. Marginal area yellow. The venation (fig. 7) shows no principle difference to the other members of the genus.

Male genitalia (Fig. 5): Vinculum large, with u-shaped saccus. Tegumen short, uncus with a broadly triangular base, otherwise slender, distinctly flattened dorsoventrally, curved ventrad, pointed. Gnathos with strong lateral arms, medial process very narrow, slightly curved parallel to the uncus, minutely dentate dorsally, pointed at tip. Juxta large, with two dorsal spines situated laterally at the posterior margin. Valva simple, broadening towards apex, without a saccular spine or other appendages, slightly ciliate. Aedeagus with a slender, sharply bent process, arising just distally to the opening of the ductus ejaculatorius. Shaft of aedeagus strongly incurved beneath this process. A curved appendage originates at the inner side of the sinus.

Female genitalia (Fig. 6): Ovipositor comparatively short, with moderately long apophyses. Ostium wide, with a bilobed sclerotized structure inside. Upper third of the ductus bursae sclerotized, with the ductus seminalis originating in the center of this region. Ductus bursae slightly broadening towards corpus, which is small and with a trace of a signum only.

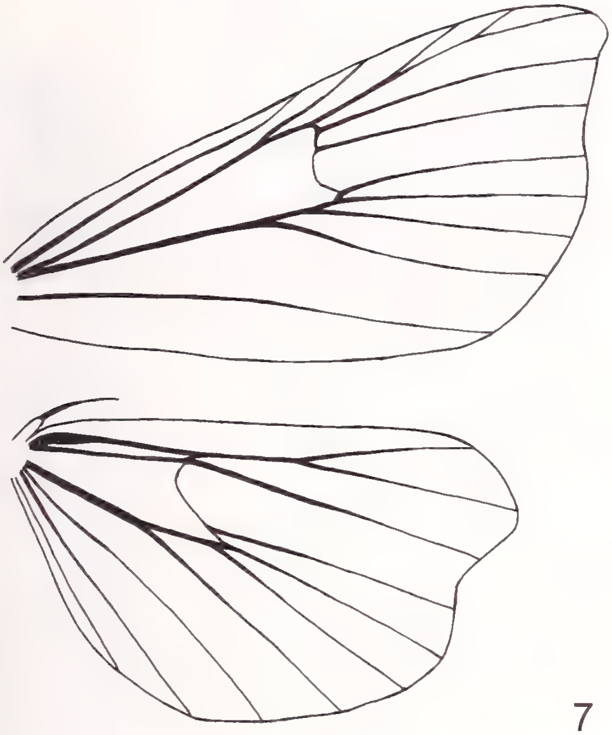

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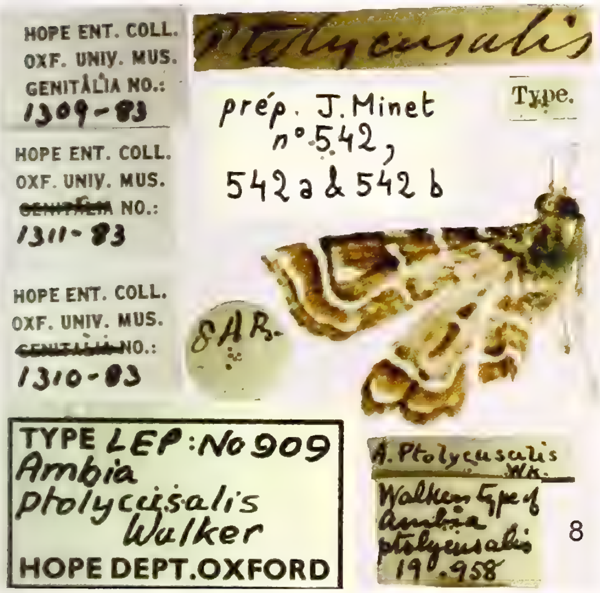
Fig. 7: *Ambia naumanni* sp. nov., wing venation.


HOPE ENT. COLL.
OXF. UNIV. MUS.
GENITALIA NO.:
1309-83
Ptolycusalis
prép. J. Minet
n° 542,
542 a & 542 b
Type.
HOPE ENT. COLL.
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1311-83
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SAR.
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Ambia
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Ambia
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Fig. 8: *Ambia ptolycusalis* Walker, 1859. Holotype with labels (Sarawak, Borneo).

The new species is very similar to the Western Palearctic *Ambia thyridialis* Lederer, which can easily be distinguished by the more brownish ground colour of the wing surface, with yellowish scales only found in the marginal fasciae. *Ambia thyridialis* Lederer is also similar in the male genitalia, lacking the saccular process of the valvae as well, but the aedeagus is completely different.

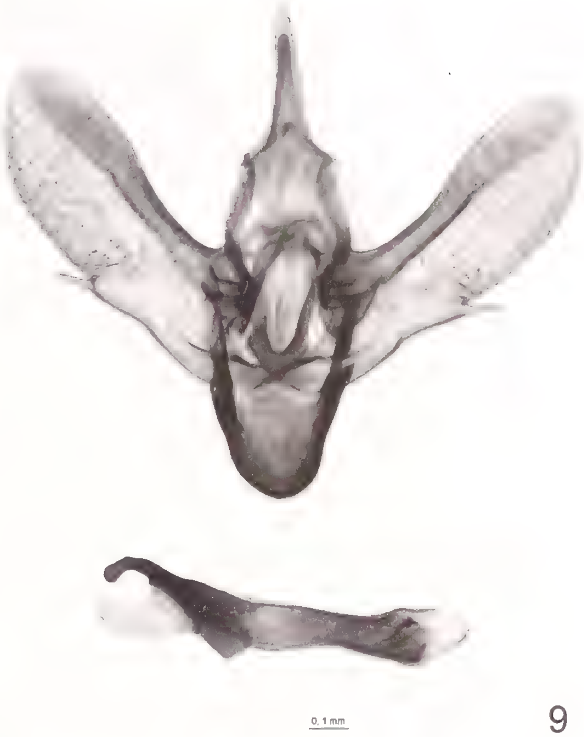

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Fig. 9: *Ambia ptolycusalis* Walker, 1859. Male genitalia of holotype.

Distribution and bionomics: Hitherto only known from the type-locality in SW. China, Yunnan, Yuelingshan near Lijiang, at elevations between 2800 and 3500 m. Flight-period from mid of June until beginning of September. First instars and foodplant unknown, but probably fern-feeding, as most of the Musotiminae are.

Acknowledgments and etymology. The new species is named in honour of Prof. Dr. C. M. NAUMANN who improved the situation in the entomological department of our museum considerably during his directorship and facilitated our work in many respects. We are grateful to Prof. Dr. K. Efetof and V. Saenko for the drawings of the genitalia and to D. J. Mann (Hope Entomological Collections, Oxford) for the loan of the type slides of *Ambia ptolycusalis*.

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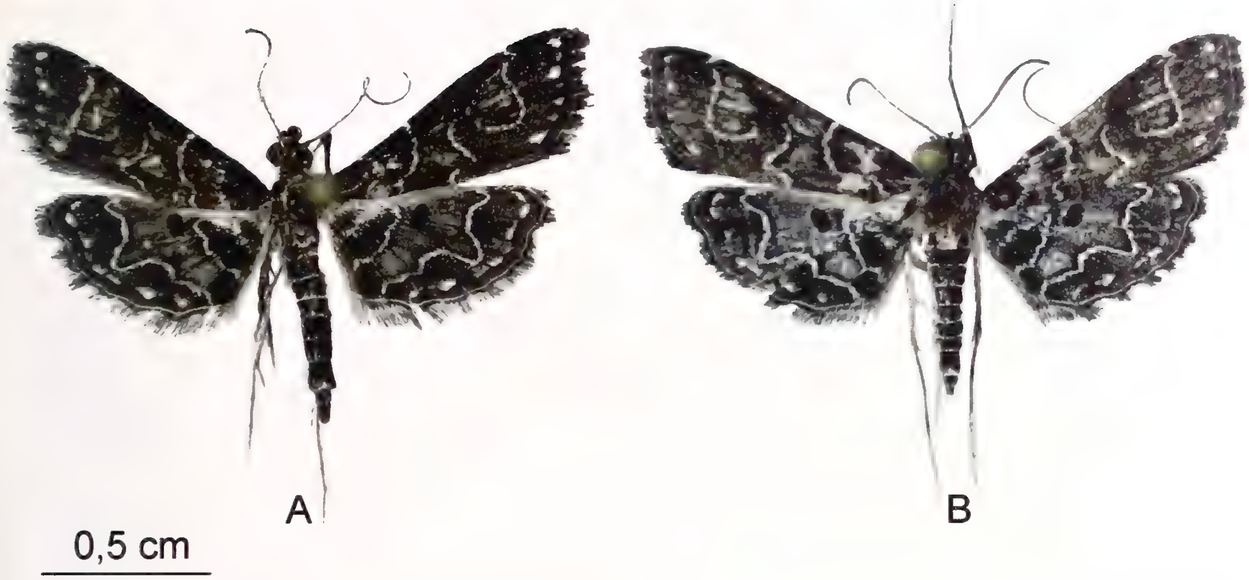


Fig. 1: *Paracymoriza naumanniella* sp. n. Holotype (male) (A) and one Paratype (female) (B). Indonesia, North Lombok, Gunung Rinjani NP, Air terjun, near village Senaru, ca. 500 - 600 m, 08°18' S / 116°24' E, 28. Dezember 2003, TF, leg. Mei-Yu Chen & Ulf Buchsbaum.

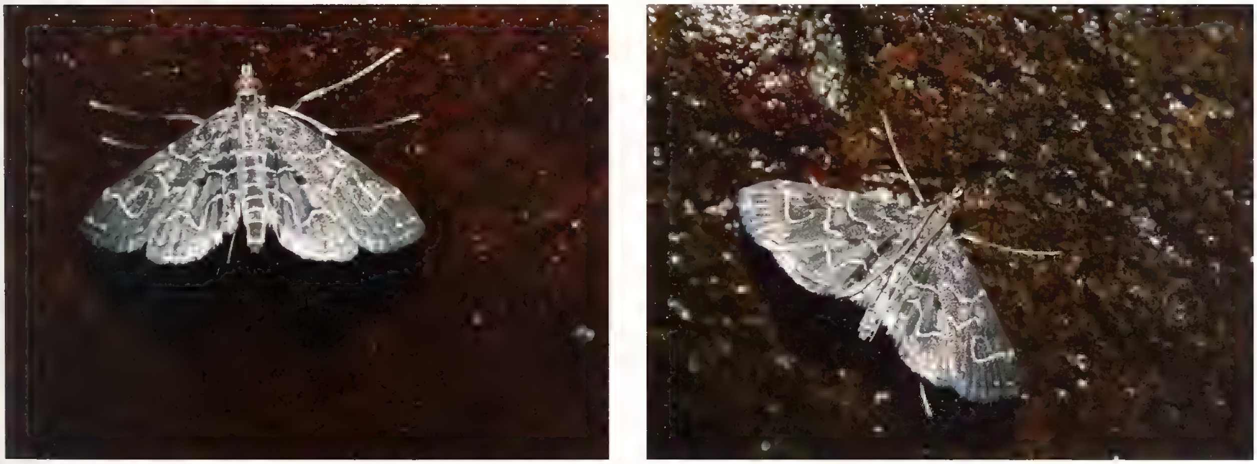


Fig. 2a-b: Paratypes of the new species still alive at the type locality in Lombok (see above). Photo: Ulf Buchsbaum.

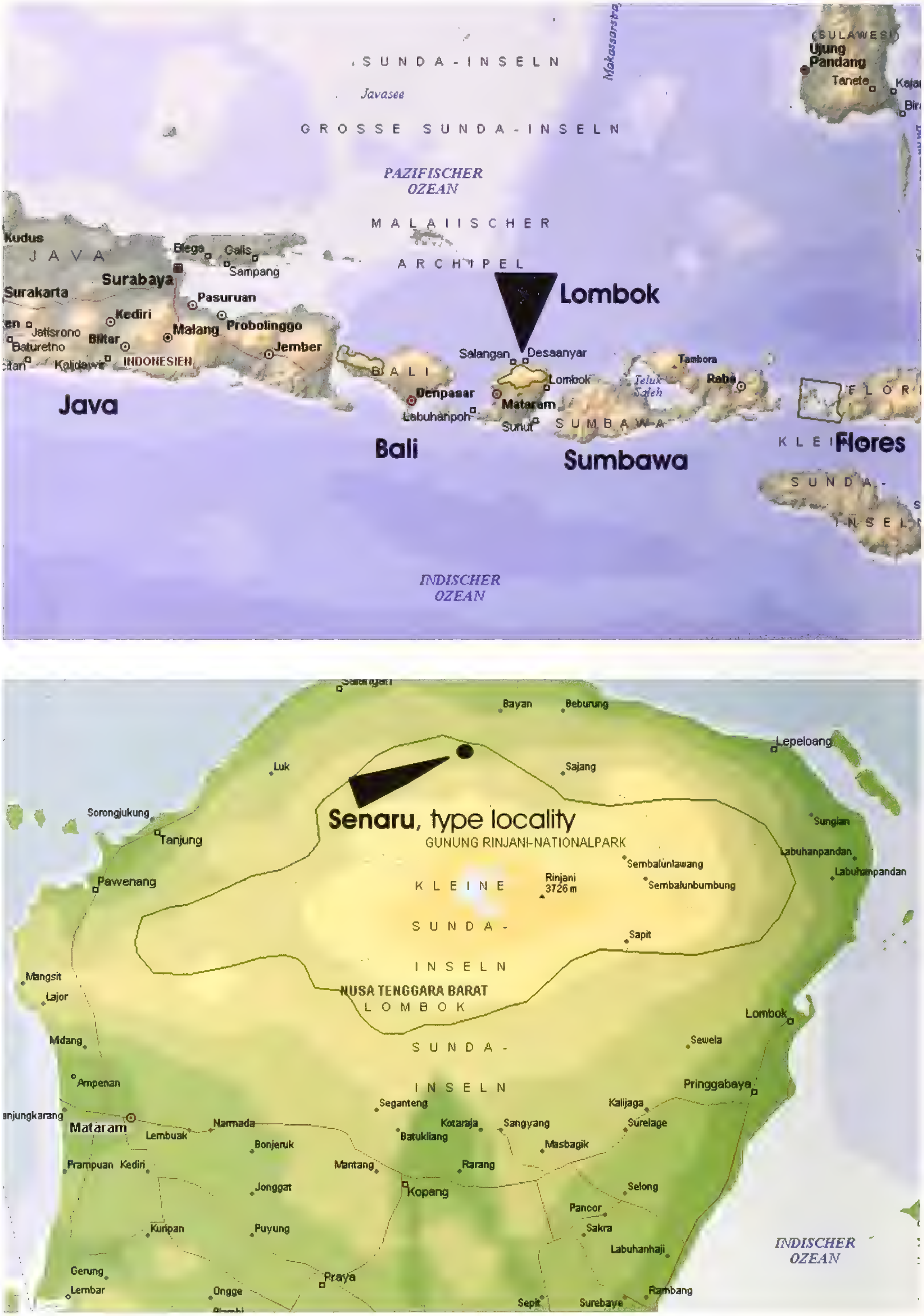
♀ *genitalia* (Fig. 4): Ovipositor short, with long, slender, fragile apophyses. Ductus bursae rather long, gradually widening towards corpus bursae, with an unusual evagination about in its middle. Corpus bursae round, ball-shaped, without a clear signum. Colliculum situated terminally, with the slender ductus seminalis originating inside and in a short distance of the colliculum. Ostial region strongly sclerotized, large, cup-shaped, narrowing strongly towards the ductus bursae.

Egg (Fig. 7a, b): Oval, with micropylar zone at the narrow end of the egg (size: 310 x 180 µm).

Distribution (maps, Figs. 5a and 5b): Hitherto only known from the type locality in Lombok.

Genetic data: We sequenced the mitochondrial gene cytochrome oxidase subunit I in order to provide a molecular dataset for subsequent re-identification of the new species as recommended by TAUTZ et al. (2003). This gene has proven its usefulness for DNA taxonomy purposes in many studies (e.g. HEBERT et al. 2003).

Genetic characterization: *Method*: DNA was extracted from abdominal tissue of some of the type specimens of *P. naumanniella* sp. nov. using Qiagen (Hilden, Germany) tissue kit according to the protocol of KNÖLKE et al. (2005). Mitochondrial (mtDNA) cytochrome oxidase subunit I (COI) gene was amplified with PCR using protocols and primers as in SIMON et al. (1994). Direct sequencing of dye labelled templates was carried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Praya
Ongge
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Fig 5: Type locality. 5 a: Enlarged view to show the situation of the Island Lombok (Indonesia) east of Bali; 5 b: type locality of *P. naumanniella* on Lombok Island near the village Senaru below the mountain Gunung Rinjani.

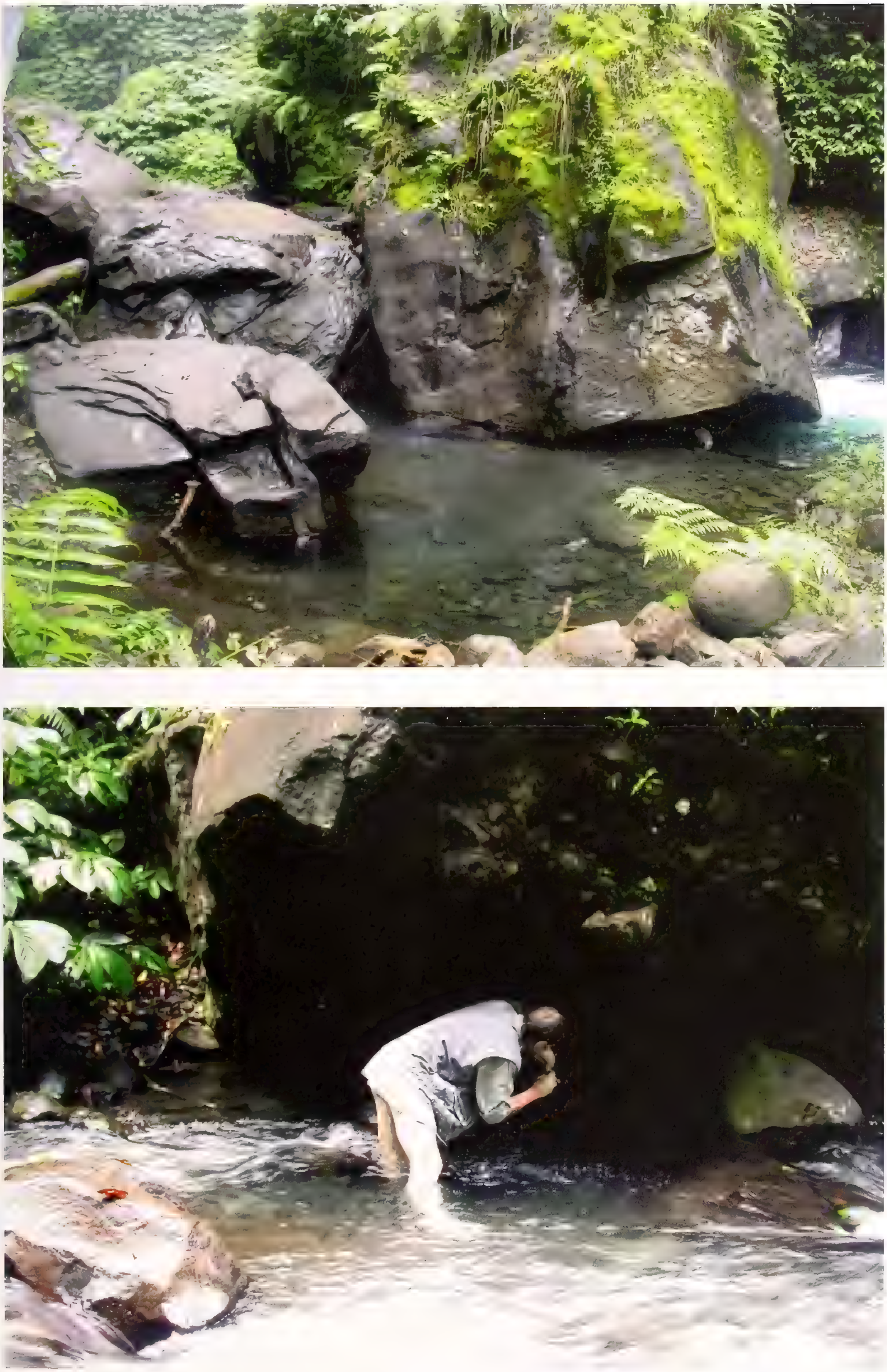
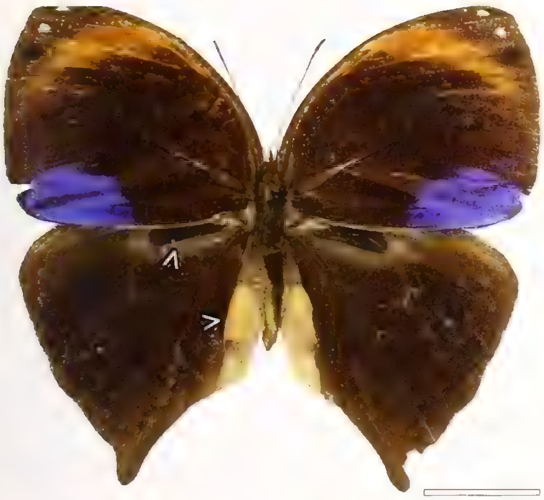


Fig. 6: Biotope at type locality beside the waterfall. 6 a: Here, most moths rest under the rocks near the water surface. Photo: Ulf Buchsbaum; 6 b: One of the authors (U. B.) collecting specimens of the new species. Photo: Mei-Yu Chen.



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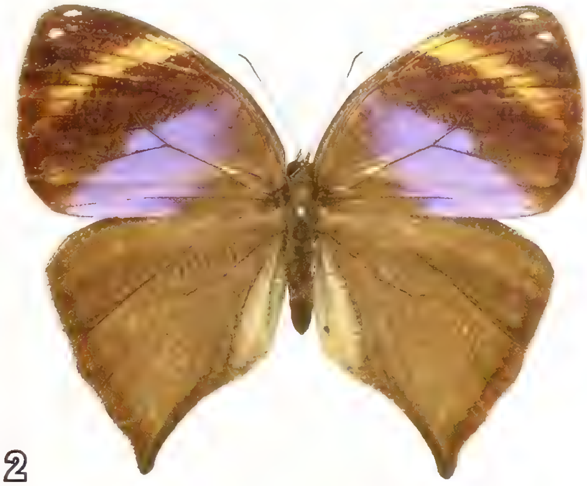

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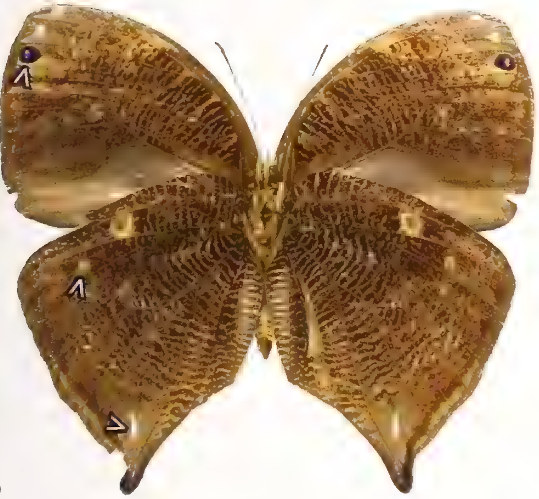

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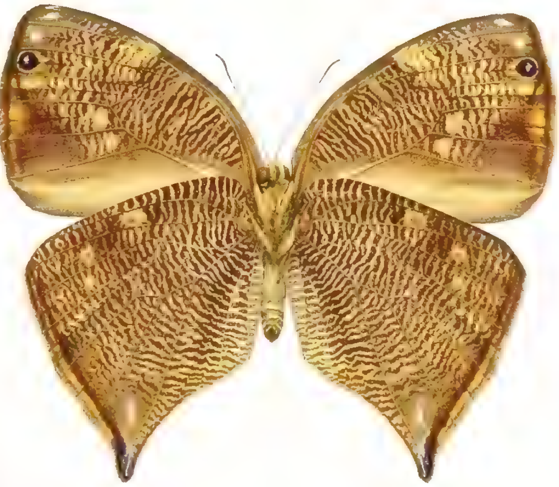

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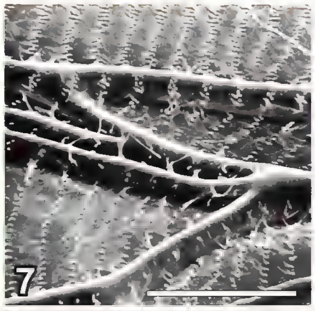

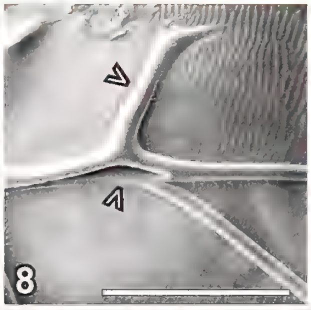

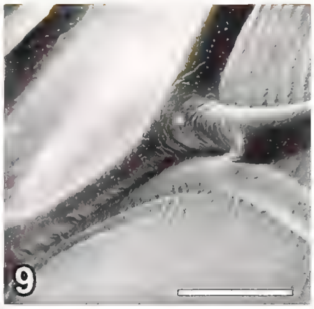

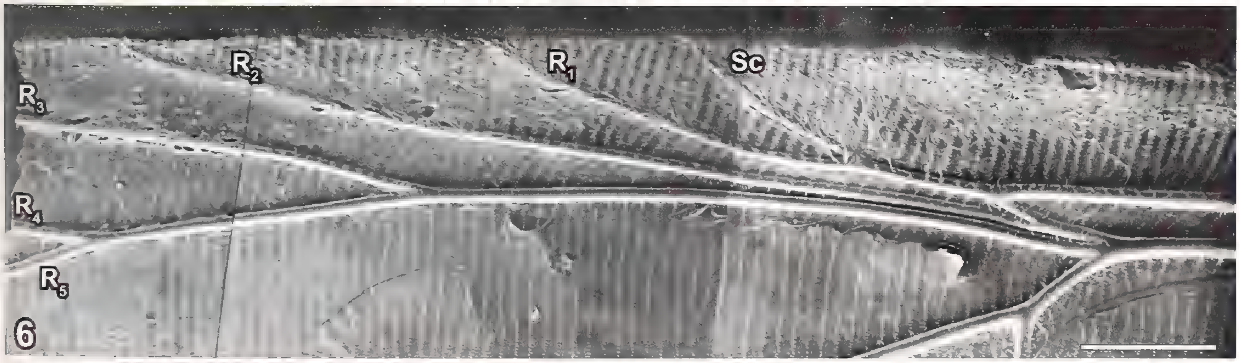
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Bonner zoologische Beiträge

Herausgegeben vom
Zoologischen
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Alexander Koenig,
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Band
54
Heft 1/2
2006 (2005)

Leibniz
Gemeinschaft

Ministerium für
Wissenschaft und
Forschung des Landes
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Bonner zoologische Beiträge werden publiziert im Eigenverlag Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn (Germany)

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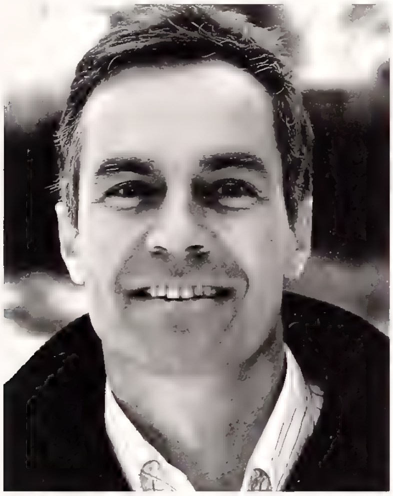
Andreas Helbig (28.07.1957 – 19.10.2005)

Prof. Dr. Andreas Helbig, member of the advisory board of Bonner zoologische Beiträge, died on 19 October 2005, at the age of only 48. He leaves a wife and two sons. His early death is a great loss not only to his family but to the scientific community, as he was a leading figure in avian science in Europe.



Andreas Helbig was an ornithologist with heart and soul. His interests in birdlife were broad, extending from bird-watching to molecular science and taxonomy, comprising field ornithology, bird migration, orientation and, more recently, molecular phylogeny and population genetics of birds. His merits are in his molecular phylogenetic publications, especially on *Sylvia* warblers, but also on birds of prey, shearwaters, gulls and other bird groups. One of his last projects was: The Herring Gull complex as a model group for recent holarctic vertebrate radiations.

His interests in birds date back to his school days in Enger, Kreis Herford, where Andreas Helbig published his first papers on observations of rare birds. From 1979 onwards he studied Biology at the University of Bielefeld, San Diego State University in California and received his Diploma on “Zugrichtung tagsüber ziehender Vögel am Teutoburger Wald, NW-Deutschland” [Migration routes of diurnal travelling birds in the Teutoburg woods, NW-Germany] at the J.W. Goethe-University in Frankfurt in 1983. After a break due to his alternative civilian service in the “Europareservat Dümmer” he continued his studies in Frankfurt. His dissertation on “Angeborene Zugrichtungen nachts ziehender Singvögel: Orientierungsmechanismen, geographische Variation und Vererbung” [Inborn migration routes of night travelling passerines: orientation mechanisms, geographic variation and inheritance] was awarded best dissertation of the year 1989. In order to learn techniques and methods for the application of molecular markers he spent several months at Queens University in Kingston (Canada), funded by the Konrad Adenauer Foundation. For a short period Andreas Helbig continued his studies on inborn orientation mechanisms in the Blackcap, *Sylvia atricapilla*, as a Postdoctoral Fellow at the Max Planck Institute for Ornithology, Radolfzell. Until 1993 he held a Postdoctoral position at the Institute of Pharmaceutical Biology, Heidelberg, financed by the German Research Foundation (DFG). From this period onwards Andreas Helbig focussed his research on molecular phylogenetics. Ornithological systematics, species concepts and those species-complexes at the transition between subspecies and species attracted his special interest. From July 1993 until his sudden and unexpected death he held the position as director of the “Vogelwarte Hiddensee” [Bird ringing center Hiddensee] at the Zoological Institute of the Ernst-Moritz-Arndt University of Greifswald. Besides his activities at the ringing station he taught “Evolution and Phylogenetics” and “Ornithology”. With his habilitation on “Molekulare Phylogenie, Systematik und Evolution der Zweigsänger (Aves, Sylviidae)” [Molecular phylogeny, systematcs and evolution of Old World Warblers (Aves, Sylviidae] in 1997 he advanced to the leading expert on avian molecular systematics over broad areas of Europe. The German Ornithologists’ Society (DO-G) awarded his research with the “Stresemann-Förderung” in the same year.

Besides his duties as director of the Institute and teacher, Andreas Helbig was active in several other fields: He was also chairman of the Scientific Committee of the DO-G, Secretary General of the European Ornithologists’ Union for five years, joined the TSC (= Taxonomic Sub-committee (TSC) of the British Ornithologists’ Union, BOU), and was well-known as a member of the German Rarities Committee for about 20 years. As editor, subject editor or member of the editorial board, he contributed to the scientific quality of several journals; e.g., “Vogelwelt – Beiträge zur Vogelkunde”, “Journal of Ornithology“, “Berichte aus der Vogelwarte Hiddensee”, “Limicola”, and “Journal of Evolutionary Biology”.

Andreas Helbig also kept contact with our Research Museum. He was on the advisory board of our institutional journal "Bonner zoologische Beiträge". He was invited speaker at the Second European Symposium on Bird Collections in November 2001 and at the 44th Phylogenetisches Symposium on adaptive radiations in 2002. The presentation of his research project on radiation in the Herring Gull complex (*Larus argentatus*-complex) by his wife, Dorit Liebers-Helbig, had to be delayed until February 2006.

I still remember the circumstances when I met Andreas Helbig for the first time. It was during the Pan African Ornithological Congress in Nairobi 1988, when everybody was spending his or her spare time in Nairobi National Park for bird-watching. Provided with the intimate knowledge of local ornithologists where to spot rare birds, we easily arrived at the best places – always to find Andreas Helbig already there. This episode exemplifies his attitude towards all fields of ornithology – his alert interest in any actual and novel event concerning birds, as well as his competency of recognizing these. His passing leaves a great gap in avian science.

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Bonner zoologische Beiträge	Band 54 (2005)	Heft 1	Seiten 3–23	Bonn, April 2006

Butterfly Diversity and Protection in Turkey

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Abstract. The aim of this paper is to demonstrate the outstanding diversity, the endemic and rare taxa, to present a model of evaluation of sites to be protected and to give some recommendations for the protection of butterflies in Turkey.

Key words. Butterfly endemism, rare butterflies, priority sites, protection management.

1. INTRODUCTION

What should be protected? – In many countries legal prescriptions exist for the protection of plants and animals. As a rule, all measures taken are directed at the conservation of individuals of a single species. Nine of the butterfly species occurring in Turkey are named in Annex II and Annex IV of the Habitats Directive and the Bern Convention. Background information on these species and their threat situation in Europe is given in VAN HELSDINGEN et al. (1996) and WAGENER (1996). The author presented data on the threat and conservation status for all butterfly species occurring in Turkey in the Red Data Book of European Butterflies (VAN SWAAY & WARREN 1999).

In spite of all efforts, the number of butterfly populations incessantly decreases. This experience is depressing for any lepidopterist working in the field, and asks for new ways.

To protect individuals of mammals and birds with a very low rate of increase surely is worthwhile, but to protect individuals of insects such as butterflies with a generally high maximum rate of fertility is scientifically unjustified and is practically not workable. By nature, insects serve as food for many predators like birds, lizards, and spiders. In an undisturbed ecosystem, a butterfly population usually shows only limited annual undulations in their density, because the population is able to compensate such losses through predators and even through unfavourable weather conditions during their life cycle. But such undisturbed habitats become rare more and more by human activities, in Turkey, and elsewhere in Europe and all over the world. The device must call: Protect the populations and their habitats before the last legally protected species has disappeared! That is in favour not only of butterflies but also of other animals and plants, too.

If one wants to protect a butterfly species one has at first to know if and where it occurs at all. Secondly one must know the biology of the species and their environmental requirements such as special climatic factors, food plants for the larvae and the butterflies, special habitat and vegetation structure and others. Thirdly, one must know what exactly threatens the existence of the species by man's activities, which disturb the balance of the ecosystem of which the species is a part of (cfr. WARREN 1992).

This paper attempts to answer the first question for Turkey. Satisfying answers to the second and third questions can be given presently for only a very few species. A lot of scientific research work of that kind that TULUHAN (1998, fig. 2) has shown in his "flowchart of an effective environmental management" has still to come for many years. The only effective protection of Turkish butterfly taxa right away is therefore the conservation of the sites in which they are still found today. The Tables and Maps herein show where to look for such sites. "Diversity", "endemisms" and "rarity" demonstrate this each in a somewhat different way but the final result is almost the same related to a certain UTM 10 km square.

2. DIVERSITY OF BUTTERFLY TAXA IN TURKEY

Species diversity is generally higher in Turkey than in any other country of Europe or the Near East, in plants as well as in animals, not only in butterflies and moths but also in other orders of insects.

The first butterflies from Turkey were described by CRAMER (1775) and HERBST (1798) in the late eighteenth century. Systematic research started in the early nineteenth century, mainly by Hungarian, Austrian and German collectors. STAUDINGER (1878-1881) already could list 199 butterfly species from about 30 localities. In the last time, especially since 1970, the exploration was strongly intensifyed by Turkish and European lepidopterists so that today 369 species or, including 79 subspecies, 448 taxa of butterflies are known from more than 2300 localities. In Appendix 1, all recognized species and subspecies of butterflies occurring in Turkey ascertained up to 2003 are listed and shows the number of UTM 10 km squares in which that taxon occurs. The list mainly is based on HESSELBARTH et al. (1995) and represents through corrections and additions the latest stand of faunistic, taxonomic and nomenclatural knowledge.

The species shared between families of butterflies are shown in Table 1. In Turkey, the family Lycaenidae has the highest number of species and the highest number of endemic species or subspecies. Almost every year new taxa are discovered whilst the number of species and subspecies in the other families now seems to be stable. The taxonomic status and the distribution of some described taxa, especially in the genus *Polyommatus* (subgenus *Agrodiaetus*) is still uncertain. Many data for species of *Agrodiaetus* therefore could not be used in this study. The different forms of *Hyponephele lycaon* are treated here as a single *lycaon*-complex, and also *Leptidea sinapis* and *L. reali* as a single *sinapis*-complex. To settle these open questions still more research is urgently needed.

Table 1. Distribution of species among the families of butterflies in Turkey

Family	Species	Subspecies	Total
Hesperiidae	41	5	46
Papilionidae	12	8	20
Pieridae	36	9	45
Lycaenidae	150	26	176
Nymphalidae	125	28	153
(Satyrinae	(72)	(23)	(95)
	369 species	79 subspecies	448 taxa

The species *Catopsilia florella* and *Hypolimnas missippus* cannot be deamed as stable elements of the Turkish fauna. They are very rare accidental immigrants from Arabia and are not taken into account in the further considerations.

To demonstrate the extraordinarily high butterfly taxa diversity in Turkey, Map 1 shows the number of species for every UTM 10 km square. The squares are enumerated according to their UTM alphanumerical codes from West to East according to the Tactical Pilotage Chart.

Data for the time between January 1951 and December 2002 were at the author's disposal for 1846 UTM 10 km squares out of 7998 possible ones for Turkey. These data were taken from HESSELBARTH et al. (1995), the data bank for Turkish Butterflies held by Harry van OORSCHOT and publications since 1994 (see references) as well as from a list of observations between 1995 and 2001 sent to the author by Lutz Lehmann.

On the basis of these data the distribution maps in HESSELBARTH et al. (1995) have been made topical. The numbers of taxa per 10 km UTM square have been gained by means of a line list. The resulted numbers from 1 up to 170 taxa/square are given in column 3 of the Appendix 2[1]. To make the map comprehensible the numbers were divided into 10 grades, each of 17 taxa. A certain colour has been assigned to each grade (see "Colour scale for number of taxa" at top of Map 1). White marks squares without any record. By using this scale, the colour grade 1 to 10 can be deemed as a "diversity weight" in favour of the corresponding square.

The squares from which a butterfly taxon is known and the number of taxa observed within one square is not evenly distributed over the country for several reasons:

- The recording level is with 23 % of possible squares moderate. From many squares only one or two species are known, the highest species number in one square is 170 (South side of Ovit Geçidi, Prov. Erzurum).
- The single parts of the country are very different in their natural provision by orography, climate, soil, vegetation, land use and other factors so that only species adjusted to special conditions can survive in certain sites or are, owing to geohistorical processes, restricted geographically to defined regions.
- Large parts of mountainous regions are hardly accessible, others suffer through overgrazing, other parts, formerly steppe land, have been converted into large monotonous wheat fields during the last decades, again other sites became lost through artificial lakes, intensification of agriculture or building especially around the large cities of İstanbul, Bursa, İzmir, Konya, Adana and along the Mediterranean and Marmara coasts. Therefore, large white spots in the map do not necessarily mean that these areas have not been explored. In fact, there are large areas in which one may hardly see any butterfly at all. The number of such sites increases from year to year.
- Usually researchers, going by car, collected butterflies mostly by the wayside, rarely 1 to 2 kilometres from a road. Sites further away, accessible only by walking or riding have been mostly neglected. Many squares have been visited only once and shortly, other places repeatedly and at different times for several days. Success of collecting depends often on the weather and to come across just with the right flying period. Large regions in the Southeast of Anatolia were prohibited to enter by military.

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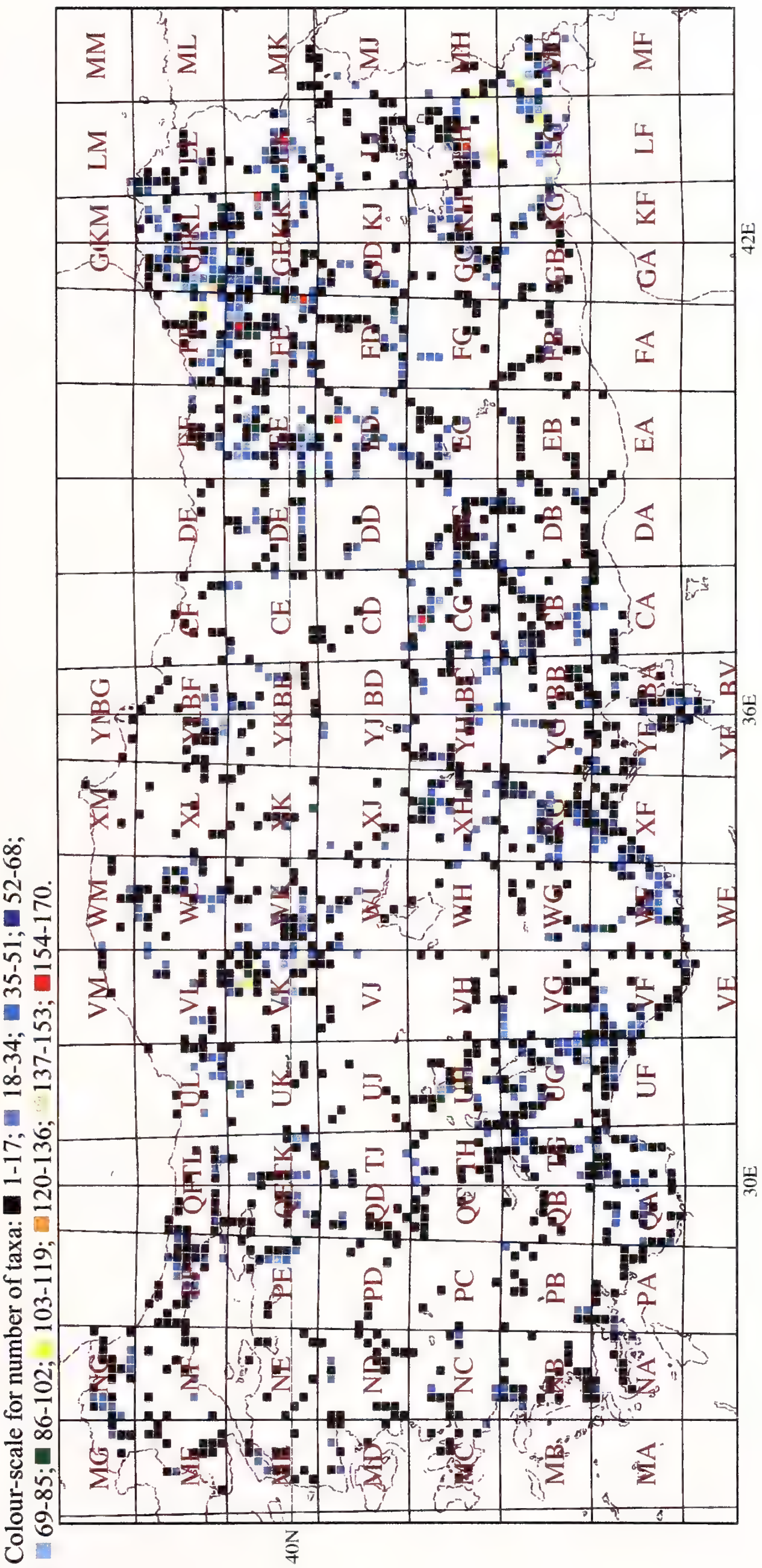
[1] The complete Appendix 2, containing all primary (total species number) and secondary data (rarity, endemicity & other weights) for 1846 UTM 10km squares evalutated can be obtained from the Lepidoptera curator of Museum Koenig.


Colour-scale for number of taxa: ■ 1-17; ■ 18-34; ■ 35-51; ■ 52-68;
■ 69-85; ■ 86-102; ■ 103-119; ■ 120-136; ■ 137-153; ■ 154-170.
40N
30E
36E
42E

Map 1: Butterfly taxa diversity in Turkey (taxa/square).

- The best explored areas can be deamed from West to East: The region of İstanbul, the surroundings of Bursa with the Uludağ, Sultan Dağları, North- and South-side of Sertavul Geçidi (provinces Içel/ Karaman), the districts of Ayaş, Kızılcahamam and Ankara (province Ankara), the area North of Saimbeyli (province Adana), Ala Dağları (provinces Niğde and Kayseri), the area of Kopdağ (provinces Erzururm/Bayburt) and Palandöken Dağı (province Erzurum), Ovit Geçidi (province Erzurum/Rize), the district of Sarıkamış, the Aras Valley between Karakurt and Tuzluca (provinces Kars and Iğdır) and the district of Posof (province Ardahan).

3. ENDEMIC BUTTERFLY TAXA IN TURKEY

Under the aspect "what should be protected", nobody will doubt that a site with high species diversity should have priority. But diversity in itself has no comprehensive significance. One must also ask for the quality of a taxon, i.e. does it occur only in Turkey or also in other countries?

The taxa so far known to be endemic for Turkey are listed in Table 2. No differences have been made between species and subspecies. Both are equally important in terms of evolution. Altogether there are 101 endemic taxa, i.e. 22.5 % of 448 known taxa in Turkey. The number of squares in which the taxon has been found gives an idea about the distribution and commonness of each endemic taxon.

Table 2. List of endemic taxa in Turkey and number of squares in which they occur

Endemic taxa	Squares
Pyrgus melotis graecus (Oberthür, 1910)	5
Pyrgus bolkariensis De Prins & van der Poorten, 1995	3
Pyrgus aladaghensis De Prins & van der Poorten, 1995	4
Archon apollinus forsteri Koçak, 1977	1
Parnassius nordmanni thomai de Freina, 1980	3
Parnassius apollo graslini Oberthür, 1891	73
Pieris bryoniae turcica Eitschberger & Hesselbarth, 1977	28
Pieris bryoniae goergneri Eitschberger, 1986	2
Pieris bowdeni Eitschberger, [1984]	13
Lycaena virgaureae aureomicans (Heyne, 1897)	8
Lycaena euphratica Eckweiler, 1989	14
Tomares nogelii obscura (Rühl, [1893])	6
Satyrium marcidum mardinum van Oorschot et al. 1985	1
Satyrium zabni van Oorschot & van den Brink, 1991	65
Satyrium myrtale armenum (Rebel, 1901)	26
Cupido minimus albocilia van Oorschot et al., 1984	8
Pseudophilotes bavius vanicola Koçak, 1977	20
Glaucopsyche astraea astraea (Freyer, [1851[)	41
Glaucopsyche astraea eckweileri Koçak, 1979	4
Jolana iolas lessei (Bernardi, 1964)	65
Turanana cytis kurdistana Eckweiler, 1984	5
Plebeius eumedon aladaghensis (Koçak, 1979)	9
Plebeius teberdinus nahizericus (Eckweiler, 1978)	2
Plebeius hyacinthus (Herrich-Schäffer, [1847])	16
Plebeius torulensis (Hesselbarth & Siepe, 1993)	1
Plebeius isauricus isauricus (Staudinger, 1871)	13
Plebeius isauricus latimargo (Courvoisier, 1913)	12
Polyommatus fatima (Eckweiler & Schurian, 1980)	14
Polyommatus myrrha myrrha (Herrich-Schäffer, [1851])	16
Polyommatus myrrha hakkariensis (Koçak, 1977)	11
Polyommatus aedon myrrhinus (Staudinger, 1901)	66
Polyommatus aedon araxianus (Koçak, 1980)	1
Polyommatus eros molleti Carbonell, [1994]	1
Polyommatus bollandi Dumont, 1998	1
Polyommatus buzulmavi Carbonell, [1992]	9
Polyommatus syriacus burak (Koçak, 1992)	14
Polyommatus dezinus (de Freina & Witt, 1983)	3

Endemic taxa	**Squares**
Polyommatus ossmar ossmar (Gerhard, [1851])	90
Polyommatus interjectus (de Lesse, 1960)	5
Polyommatus antidolus (Rebel, 1901)	18
Polyommatus kurdistanicus (Forster, 1961)	7
Polyommatus menalcas (Freyer, [1837])	144
Polyommatus hopfferi (Herrich-Schäffer, [1851])	80
Polyommatus poseidon poseidon (Herrich-Schäffer, [1851])	89
Polyommatus putnami Dantchenko & Lukhtanov, 2002	2
Polyommatus dama dama (Staudinger, 1892)	2
Polyommatus maraschi Forster, 1956	1
Polyommatus damocles kanduli Dantchenko & Lukhtanov, 2002	1
Polyommatus cilicius cilicius Carbonell, 1998	2
Polyommatus cilicius bolkarensis Carbonell, 1998	4
Polyommatus sertavulensis (Koçak, 1979) (stat. inc.)	6
Polyommatus ernesti Eckweiler, 1989 (stat. inc.)	3
Polyommatus artvinensis (Carbonell, 1997)	13
Polyommatus bilgini Dantchenko & Lukhtanov, 2002	3
Polyommatus haigi Dantchenko & Lukhtanov, 2002	4
Polyommatus sigberti Olivier et al., 2000	24
Polyommatus lycius (Carbonell, 1996)	4
Polyommatus pierceae Lukhtanov & Dantchenko, 2002	1
Polyommatus erzindjanensis Carbonell, 2002	1
Polyommatus turcicolus (Koçak, 1977)	17
Polyommatus guezelmavi Olivier et al., 1999	1
Polyommatus theresiae Schurian et al., 1992	1
Polyommatus surakovi sekercioglui Dantchenko & Lukhtanov, 2002	1
Polyommatus carmon carmon (Herrich-Schäffer, [1851])	48
Polyommatus carmon munzuricus (Rose, 1978	2
Polyommatus schuriani (Rose, 1978)	13
Polyommatus anticarmon (Koçak, 1983)	9
Polyommatus huberti (Carbonell,1993)	39
Polyommatus turcicus (Koçak, 1977)	37
Polyommatus merhaba De Prins et. al., 1991	15
Polyommatus iphicarmon Eckweiler & Rose, 1993	1
Polyommatus tankeri (de Lesse, 1960)	10
Polyommatus baytopi (de Lesse, 1959)	13
Argynnis paphia delila Röber, 1896	14
Argynnis aglaja ottomana Röber, 1896	23
Argynnis adippe taurica Staudinger, 1878	16
Boloria graeca karina van Oorschot & Wagener, 1990	2
Coenonympha leander dierli Koçak, 1977	2
Hyponephele urartua de Freina & Aussem, [1987]	8
Hyponephele naricina naricoides Groß, 1977	17
Hyponephele kocaki kocaki Eckweiler, 1978	4
Hyponephele kocaki melesina Weiss & Skala, 2000	5
Hyponephele cadusia zerneca Skala, 2003	3
Erebia ottomana ottomana Herrich-Schäffer, [1847]	6
Melanargia syriaca syriaca (Oberthür, 1894)	14
Melanargia syriaca kocaki Wagener, 1983	35
Melanargia grumi Standfuss, 1892	60
Melanargia titea wiskotti Röber, 1896	22
Melanargia larissa noacki Wagener, 1983	196
Melanargia larissa massageta Staudinger, 1901	11
Melanargia larissa taurica Röber, 1896	104
Satyrus favonius favonius Staudinger, 1892	57

Endemic taxa	**Squares**
Chazara egina egina (Staudinger, 1892)	11
Chazara egina aisha Rose, 1986	3
Pseudochazara lydia lydia (Staudinger, 1878)	24
Pseudochazara lydia obscura (Staudinger, 1878)	29
Pseudochazara lydia aurora Eckweiler & Rose, [1989]	32
Pseudochazara mamurra mamurra (Herrich-Schäffer, [1846])	56
Pseudochazara mamurra birgit Groß, 1978	30
Pseudochazara mniszechii mniszechii (Herrich-Schäffer, [1851])	152
Pseudochazara anthelea selcuki van Oorschot et al., 1987	8

In the fifth column "endemisms" of Appendix 2(see Footnote 1), the number of endemic taxa occurring in the corresponding square is named. The distribution of the endemisms is shown in Map 2 "endemisms/square". Two squares (FE68 southside of Ovit Geçidi, province Erzurum, and LH31 10 km N Çatak, province Van) each bear with 16 taxa the highest number of endemisms. To make the map more impressive, this number has been divided into 10 colour grades as indicated at the top of Map 2. These colour grades are listed in Appendix 2 (see Footnote 1) in column 6 "weight 2".

Map 2 shows the distribution of squares with endemisms over the country. Generally, the number of endemisms per square is higher from West to East. The 101 endemic taxa are spread over Anatolia with concentrations in the Southwest, Northeast and Southeast. These concentrations are the result of processes of repeated glacial displacements and postglacial recolonizations and connected with the fact that the endemisms occur today in or nearby former refuges in which they could survive the different pleistocene glacial periods. In the Mediterranean region these refuges are valleys on the southside of the Taurus mountains and the coastal areas along the Mediterranean Sea southward up to Lebanon and Israel. In Northeast, Anatolia postglacial recolonization has taken place mostly from the kolchic refuge in today's Republic of Georgia and the climatically favoured Çoruh Valley. Many of the here existing taxa are rare Caucasian elements not occurring in other regions of Turkey. In Southeast Anatolia, south of Lake Van, the deep gorges of Botan, Harbur and Zab with her rich vertical structures formed a favourable refuge for numerous Tertiary relicts and elements of the Turk-Iranian Zagros fauna and flora, which do not exist in other Turkish regions.

4. RARE BUTTERFLY TAXA IN TURKEY

With the previous actions only the species diversity has been treated in two different ways. But also the rarity of the taxa must be taken into consideration under the aspect of the protection of sites.

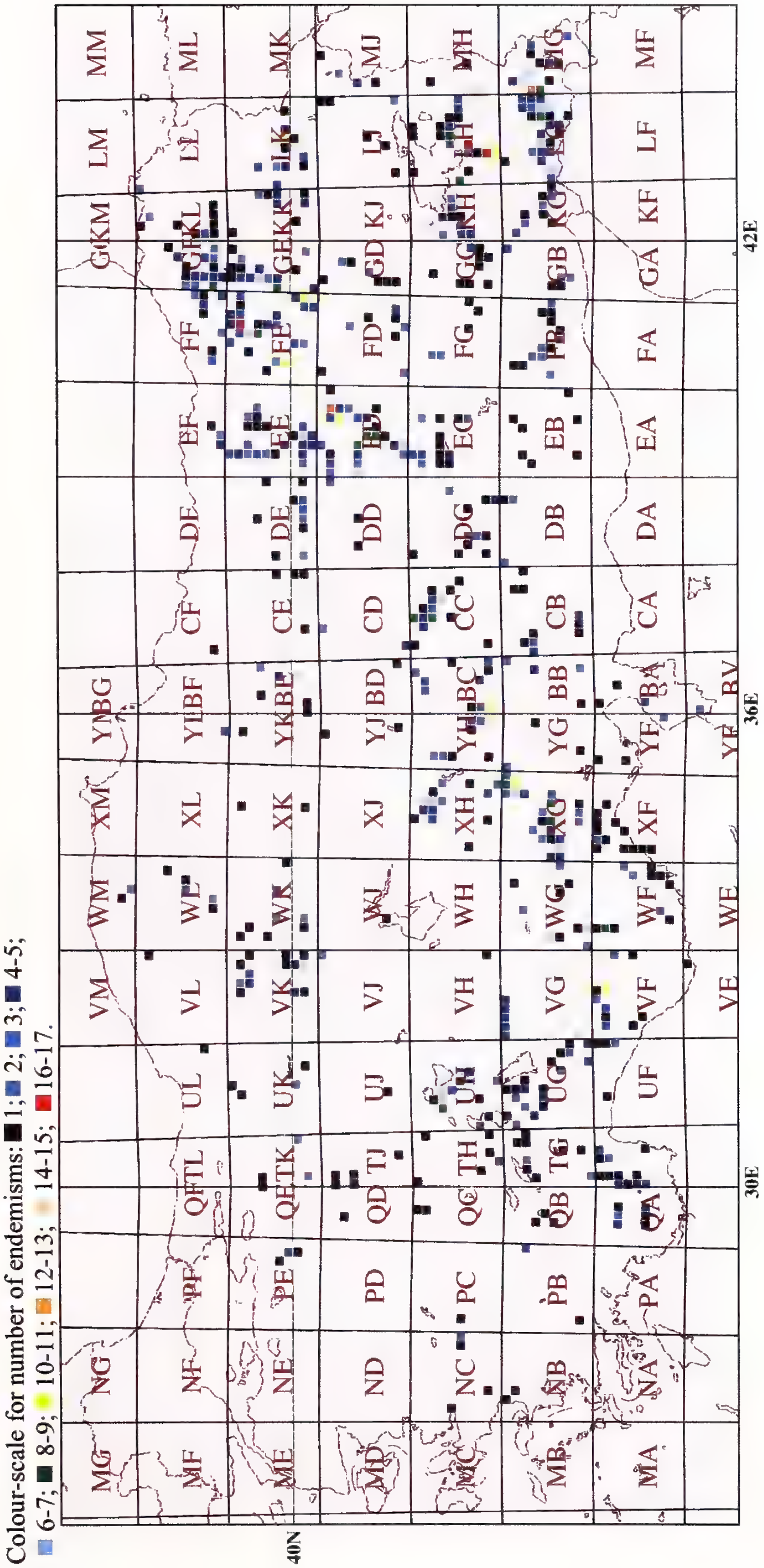
In the list of butterfly taxa occurring in Turkey, there has been said from how many squares the taxon is known. If a butterfly taxon occurs only in up to 50 squares – that are about 10 % of the highest numbers of squares (more than 500) – it can be deemed as rare in Turkey. All taxa with an occurrence in 51 or more squares remain unconsidered, equally valid for endemic as well as non-endemic taxa.

In column seven "rare taxa" of Appendix 2 (see Footnote 1), the number of such rare taxa in the corresponding square is given independently from the number of squares in which the taxa have been found elsewhere. But it is easy to understand that there is quite a difference if a taxon occurs only in one square at all or in fifty squares. Therefore a scale has been used to weight the difference in the occurrence of a taxon in one up to fifty squares through 10 grades of "rarity points" according to the scheme for each taxon (see Table 3).

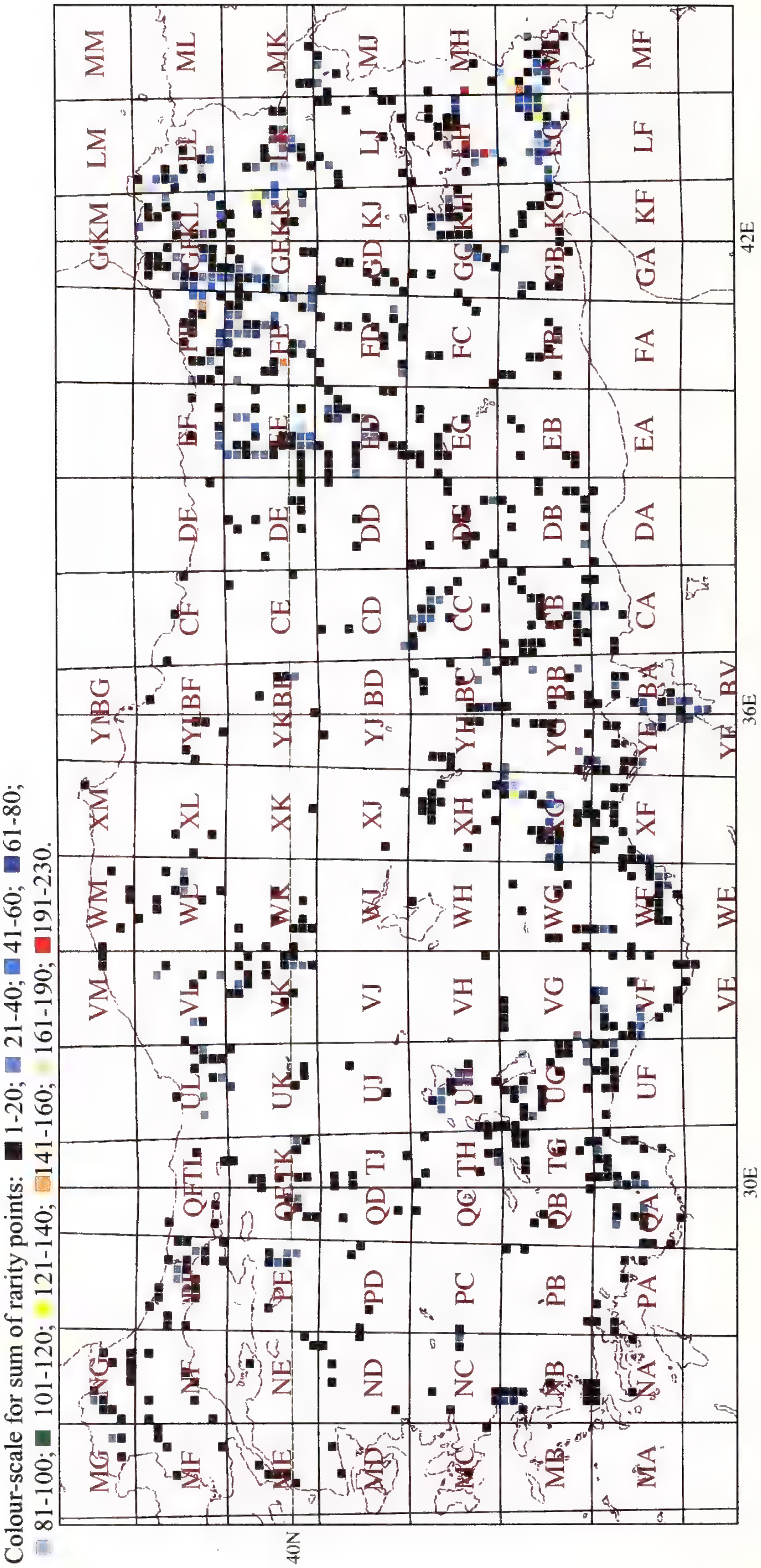
Table 3. Scheme for the calculation of "rarity points"

Number of squares / rare taxon	**Rarity points**	**Number of squares / rare taxon**	**Rarity points**
50 – 43	1	20 – 16	6
42 – 36	2	15 – 12	7
35 – 31	3	11 – 8	8
30 – 26	4	7 – 4	9
25 – 21	5	3 – 1	10

If a square holds more than one rare taxon it gains for each taxon the rarity points connected to it. The summarized rarity points for each square are shown to the left in column eight "weight 3" in Appendix 2 (see Footnote 1). For the demonstration of rarity in Map 3, the sum of rarity points has been attributed to 10 colour grades as indicated in the "color scale for sum of rarity points" at top of Map 3. The numbers gained by that way represent the rarity "weight 3" of each square as shown to the right of column eight in Appendix 2 (see Footnote 1).


Colour-scale for number of endemisms: ■ 1; ■ 2; ■ 3; ■ 4-5;
■ 6-7; ■ 8-9; ■ 10-11; ■ 12-13; ■ 14-15; ■ 16-17.
40N
30E
36E
42E

Map 2: Geographical and numerical distribution of endemic taxa in Turkey (endemisms/ square).


Colour-scale for sum of rarity points: ■ 1-20; ■ 21-40; ■ 41-60; ■ 61-80;
■ 81-100; ■ 101-120; ■ 121-140; ■ 141-160; ■ 161-190; ■ 191-230.
40N
30E
36E
42E

Map 3: Rarity weights/square.

5. PRIORITY SITES FOR THE PROTECTION OF BUTTERFLIES IN TURKEY

In a further step, to summarize the results, "weight 1", "weight 2" and "weight 3" of Appendix 2 (see Footnote 1) were added and set to the left in column nine "sum" of Appendix 2. To demonstrate the result in Map 4, the gained values have been attributed to 10 colour grades as indicated in the "Colour scale for sum of weight points" at the top of Map 4. The colour grades 1 to 10 represent the priority of a square for the protection of butterflies in Turkey and are shown to the right in column nine in Appendix 2.

Generally, all squares with high values of more than 5 priority-weight-points (Appendix 2: column "sum", right) can request for priority in the achievement of protection measures. But that level is almost too low for eastern squares and too high for western ones. In western and Central Turkey only a few squares reach such a level of 5 priority points, and endemisms which occur only in one or a few more western squares without a high number of accompanying rare species would not have – on the base of the analysis given above – any chance for protection because they never can stay against squares with a high diversity and a high number of endemisms and rare species in eastern Anatolia. Therefore it is necessary to differentiate in the assessment of the value of protection in the different regions of Turkey. Thus it seems to be appropiate to start from a level of 3 priority points in all western und central provinces of Turkey in choosing sites for protection. In any case, a site with very rare endemism should have priority even if the square inhabited by that endemism does not even reach the level of 3 points. Every such square and endemic taxon occurring in it asks for highest attention by the provincial and local proper authorities concerned with nature protection. Examples for such cases are given below:

Archon apollinus forsteri KOCAK, 1977, only occurrence in square WM50, province Kastamonu, Ödemiş south of Küre, priority points: 2;

Polyommatus dama dama (STAUDINGER, 1892), only two squares: DC32, province Malatya, south of Yeşilyurt, priority points: 2 (see WAGENER in VAN SWAAY & WARREN 2003), and square DC71, province Adıyaman, north-side of Nemrut Dağı, priority points: 2.

The sites are mostly not identical with the whole area of a square but only with a part of it. Hence the square code can give only a rough indication that in that square exists one or more sites with a high claim for protection. Therefore, the sites have to be explored and exactly defined before any measures can be taken.

6. RECOMMENDATIONS

Each butterfly species is embedded in a special environment to which it is adapted and from which it is more or less strongly dependent. The relations are mostly very complex and different for each species. Most of the butterflies like sheltered open sunny places with a rich structure of edges of forests, coppices, hedgerows, grassland, fields, rides, glades or erosion gullies which offer the opportunity for patrolling, perching or hilltopping and mating. A few prefer the shade of a wood. Not so few need a special foodplant for their larvae, others are more stenophagous or even polyphagous. Many nectar-offering flowers are vitally necessary for the butterflies. The males of most species must have the opportunity to suck minerals on wet soil to raise their fitness and the fertility of the copulating female.

One may assume that the sites in squares with a high species diversity basically still fulfil all these requirements, but one should not overlook the threats and declines of Turkish butterflies, ultimately caused by habitat changes or loss of habitats (see WAGENER in VAN SWAAY & WARREN 1999).

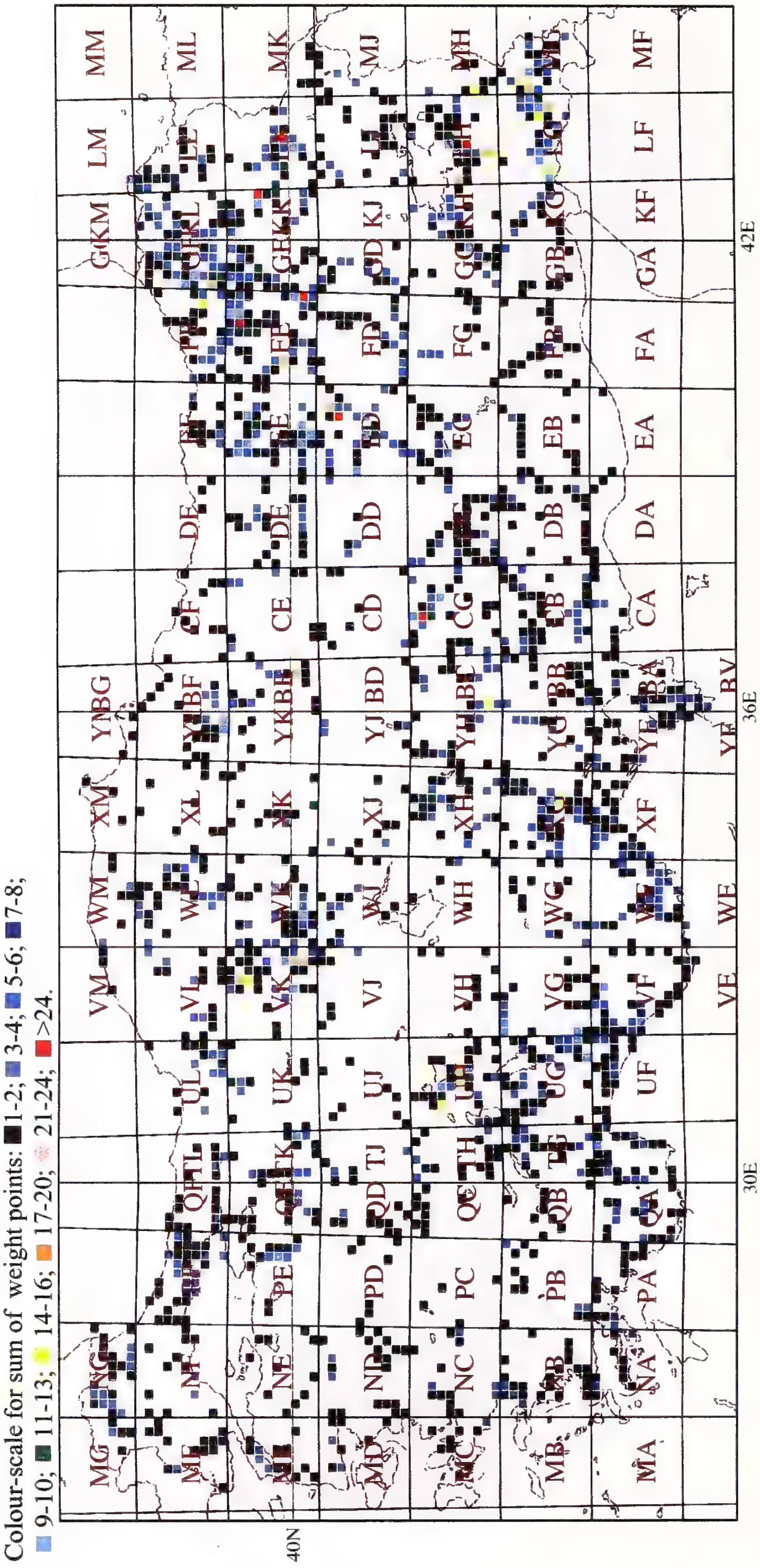
It may be allowed to the author to name some threats and to give some special recommendations on the base of his own observations.

6.1. To the address of forestry commissions

Almost every provincial capital in Turkey has today its own "Milli Parkı", a place of woodland, old ones or new afforestations, controlled by the forestry commission. As a rule these National Parks are valuable sites for butterflies but they suffer under a high recreation pressure of the nearby population especially on the weekends of summer months through wild picnicing destroying the low vegetation and leaving behind rubbish.

On the Kayatepe Geçidi on the border of provinces Kastamonu/Çorum between Tosya and İskilip existed in an oakwood an isolated population of *Melanargia larissa lesbina* of particular biogeographic interest. In 1988 this oakwood was found clear-cut and the population through such a radical change of its habitat destroyed. To avoid such unintended threats, the forestry commissions should generally use the selection forest method only.

Experience shows that with the afforestation of an area the low vegetation, before degraded by overgrazing, develops very soon and plentiful which is followed by many butterfly species finding new suitable habitats here. This was observed for example in the new Atatürk Ormanı west of Konya. When the young trees become


Colour-scale for sum of weight points: ■1-2; ■3-4; ■5-6; ■7-8; ■9-10; ■11-13; ■14-16; ■17-20; ■21-24; ■>24.
MG NG VM WM XM YMBG GKM LM MM
ME NF QFL UL VL WL XL BF CF DE EE GKL LL ML
ME NE PE QEK UK VK WK XK YKBE CE DE EE FF GEKK MK
MD ND PD QD TJ UJ VJ WJ XJ YJ BD CD DD ED FD GD KJ LJ MJ
MC NC PC QC TH UH VH WH XH YH BC CG EC FG GC KH LH MH
MB NB PB QB TG UG VG WG XG YG BB CB DB EB FB GB KG LG
MA NA PA QA UF VF WF XF YF BA CA DA EA FA GA KF LF MF
VE WE YE BV
40N
30E
36E
42E

Map 4: Priority sites for the protection of butterflies in Turkey.

higher and grow more densely together the low vegetation disappears more and more and, for many butterfly species slowly but surely comes the end of their existence. The forestry commissions should give the threatened butterflies in consequence of the changes in their habitat the chance to survive by not closing small naturally developed clearings and, under circumstances, enlarge such clearings or create some more by taking away some trees. This correlation could be well observed in the Çamlık Milli Parkı, south of the town Yozgat, where within the dense oak and pine wood only very few butterfly species could be found whilst a lot of them could be seen on the top of the hill on open grassy places between single young pines. For the conservation of butterflies this is a very important matter. The *Pinus sylvestris*-wood between Sarıkamış and the Aras valley in the province Kars is only so rich in butterfly species, because there are closed pine-stands always between smaller and larger wet or dry meadows. If the proper forestry commission does not wish to destroy this unique species diversity of 144 taxa it should do without afforestation of the open areas and take care that these meadows be cut once every year not before mid of August. The same should be done to the meadows along the road from Sarıkamış to Handere (Karaurgan) (province Kars), the pine wood north of Hanak (province Ardahan) as well as the pine wood along the road to Kütlü southwest of Göle (province Erzurum) and in all other similar places all over the country. It is to be seen with respect to Turkish forestry authorities making every effort for culturing existent woods and afforestation in struggle against soil erosion; it would be very appreciative, if they would do the same for the conservation of butterflies and through that of many other animals and plant species.

6.2. To the address of the proper authorities for land use and agriculture

Overgrazing by sheep, goats and cattle is a long known problem in Turkey not only because of the destruction of the vegetation and following soil erosion caused by this, but also because of one of the heaviest threats to butterflies and other insects as well as to the soil fauna especially in higher mountains anyway already with sparse vegetation. If one wishes to protect a site for butterflies it is unevitable to reduce overgrazing to extensive grazing. To stop grazing at all would not be desirable in any case as vegetation could grow too high, which is not favourable for numerous butterfly species. This must be considered from place to place and from species to species one wishes to protect.

Where meadows are cut once a year as a traditional way of land use, this should be maintained. The life cycle of the butterflies is adjusted to such a form of land use and any change would cause heavy damage and loss of species. It is only to take care that cutting of the meadows does not begin before mid August. That's when the butterflies – mostly Blues, Fritillaries and Satyrines – inhabiting such sites have their flying period between 10th July and 10th August. The butterflies otherwise would not find enough flowers for nectar with the consequence of lower fertility and lower egg-laying rate, if cutting occurs too early.

Thorn-cushion forming species of the plant genus *Onobrychis*, *Astragalus* and *Astracantha* are typical of high mountain steppes and are food plants of some Clouded Yellows (*Colias*) and numerous Blues of the genus *Polyommatus* especially in southeastern Anatolia. In 1985, it could be observed on the northside of Güzeldere Geçidi (province Van) at about 2500 m that a large area of the slope covered with that plant formation had been destroyed through deep ploughing with a tractor not slope-parallel but from top downhill. Such a dangerous behaviour has not only taken away the habitat for the plants and the insects living on them, but has also opened the way for severe soil erosion. The thorn-cushion plant-formation might be useless for agricultural purposes, but they are very important for soil preservation, and vital for many very rare insects in Turkey. This ought to be urgently taken into consideration when areas shall be arranged for the conservation of butterflies.

In valleys of mountainous regions the slopes on either side of a road are very often preferred habitats for numerous plant and insect species. It could be observed several times that with widening out or new constructing of such roads soil material, stones and rocks were taken from the slope above the road and tipped on the other side downward the slope. Through such a procedure the flora and fauna of both sides of the new road were deleted for a long time and along large distances. Already in the planning stage of a new road it should be deliberated how to minimize the damage and to preserve as much as possible of the present vegetation and the animals living thereon. Otherwise many rare species may be lost from that valley even forever. By such a way the populations of the butterfly *Euapatura mirza* living on *Zelkova carpinifolia*, a Tertiary relict, and of the very rare moth *Brahmaea ledereri zaba* whose caterpillars feed on *Fraxinus* in the Zab valley (province Hakkari) have been heavily threatened in connection with the construction of the new road from Hakkari to Çukurca. Rivulets along the roads should be preserved in any case to ensure that male butterflies can supply their needs for water and minerals.

6.3. Specific localities or regions

These rather general recommendations can be strengthened by aspects considering individual places or areas:

WAGENER (in VAN SWAAY & WARREN 2003) has identified five areas for eight target-species occuring in Turkey out of 34 in Europe dealt with in the Project "Prime Butterfly Areas in Europe": *Pyrgus cirsii*, *Zerynthia caucasica*, *Parnassius apollo*, *Lycaena ottomanus*, *Maculinea arion*, *Maculinea nausithous*, *Polyommatus dama*, and *Euphydryas aurinia*. The five areas are: a site 10 km SSE of Yeşilyurt, prov. Malatya; Dimçay Valley near Alanya, prov. Antalya; Kopdağı Geçidi, prov. Bayburt and Erzurum; Palandöken, prov. Erzurum; Ovitdağı Geçidi, Prov. Erzurum and Rize. For the last three areas also see below.

Belgrad ormanı. Thanks to the forestry authorities the Belgrad ormanı in todays Greater Istanbul is the only place where nature has still a chance to survive (square PF65 in Appendix 2). But even here some rare butterfly species like *Pyronia cecilia* and *Nemeobius lucina* seem to have become extinct during the last thirty years. The understandable search for recreation of the town's people should be directed and controlled to less vulnerable parts of the wood. Protection should also include the conservation of small grassy open places with only one cut of the meadows in late summer.

Uludağ near Bursa (2543 m). It is recommended to enlarge the Milli Parkı to the whole area of the Uludağ comprising the squares PE73, PE74, PE82 and PE83 (see Appendix 2) including Soğukpınar to a nature reserve. To satisfy recreation pressure, the place between the forester's lodge and the sanatorium at about 1550 m NN on the westside, the plateau north of the summit nearby the funicular from Bursa and the sporting centre as well as the immediate surrounding of the hotels at about 2000–2100 m NN should be excepted. From a lepidopterological point of view the closed *Abies* wood is not such a valuable place for butterflies except small clearings for *Parnassius mnemosyne,* but the summit region of Uludağ above treeline with the *Nardus stricta* meadows on the northside and the rocky and stony parts on the southside claim for absolute protection and should be held free from recreation during the snowless time of the year. Here are the habitats of the rare butterfly species, *Pieris bryoniae turcica*, *Plebeius pyrenaicus dardanus*, *Plebeius hyacinthus* (type locality), *Erebia ottomana ottomana* (type locality), *Pseudochazara beroe beroe* (type locality), *Parnassius apollo* and other butterflies. But even the area between Osman Gazı and Soğukpınar (500 – 1400 m) on the westside of Uludağ bears numerous other rare butterfly species and is the only locality in Turkey for *Pseudochazara mniszechii tisiphone*. To save the nature of Uludağ with its unique relict fauna, permission to build more hotels and skilifts for winter sports should not be granted.

Sultan Dağları. The Sultan Dağları, a mountain up to 2610 m NN situated in the provinces Afyon, Konya and Isparta between the towns Çay and Doğanhisar offers themselves to the creation of a Nature Reserve. Especially the valleys open to the plain on the north- and eastside and the summit region, including the pass road from Akşehir/Engilli to Bağkonak, are inhabited by a very rich flora and fauna with several endemisms and rare butterfly species (see squares UH26, UH32, UH36, UH45, UH46, UH50, UH53, UH54, UH63, UH64 in Appendix 2). The mountain is nearly unsettled. Settlements, small villages and towns follow the foot of the mountain to the plain of Konya. During summer the zone above treeline serves sheep as pasture. Grazing should be restricted before damage to the vegetation and soil becomes apparent.

Abant Gölü southwest of Bolu. Abant Gölü (UK59) and Abant valley (UL60 in Appendix 2) in the province Bolu are two sites, geographically connected with each other, with a number of rare plant and butterfly species. The place is threatened by a high recreational pressure already apparent by an alarming decline of several species like *Zerynthia caucasica*, *Pieris bryoniae turcica*, *Erebia aethiops aethiops* and others. The forestry authorities have done well to concentrate the search for recreation, especially for children, to a restricted area. The danger is that along the valley and around the lake might be set up a lot of small "lokantası" (restaurants) – as has already happened in the Dimçay valley near Alanya (province Antalya) – and that some more hotels might be erected. It would mean the death of the particularly delightful scenery of this area and the extinction of more than one rare plant and animal species. That should be avoided in any way.

Sertavul Geçidi. This pass on the road from Karaman to Silifke (border of the provinces Karaman and İçel) (WF28 in Appendix 2) offers habitats for 9 endemic and 12 rare butterfly taxa and claims for protection with priority. Meadows especially on the Karaman side of the pass should by no way be changed into arable land. Extensive grazing or grass cutting once a year in late summer would be enough to preserve this place.

Pine wood north of Saimbeyli. About 10 to 15 km north of Saimbeyli (province Adana) a large pine wood extends on both sides of the road to Tufanbeyli, 1400–1550 m NN, which is lepidopterologically already a historical place under the name "Hadjin"; it is still today a valuable habitat for 11 endemic and 15 rare butterfly taxa (see square BC41 in Appendix 2) and the only locality for *Polyommatus theresiae*. The site does not seem to be threatened by maintaining the small open places and present use as selection forest and occasional extensive grazing by sheep. But it is to be assumed that in the course of time recreational pressure will occupy the wood. The forestry authorities should recognize this threat in good time and direct the pressure to the most southern part of the wood.

Kopdağ. The Kopdağ (2963 m NN) on the border between the provinces Bayburt and Erzurum (square FE23 in Appendix 2) gleams through high diversity (10 endemic and 37 rare butterfly taxa). The whole area should get the status of a nature reserve upwards an altitude of about 1750 m NN because it is extraordinary rich in wet and dry ecological structures with different plant associations and insect communities. To preserve this unique place, the traditional land use through grazing by sheep on the southern slopes (prov. Erzurum) and cutting on western slopes (prov. Bayburt) should be maintained, grazing by cattle and the change to arable land should strongly be forbidden. Sheep grazing should not be intensified rather extensified in regard to the present state.

Ovit geçidi. The whole valley from Yukarı Özbağ in the Çoruh valley upward to the provincial border of Erzurum recommends itself for nature reserve (squares FE68, FE69, FE59 in Appendix 2). It possesses the highest number of butterfly taxa and endemisms in Turkey with 33 rare species. The slopes are downward from the village Çayırözü so steep that they can hardly be used for any purpose. Settlements are nearly missing, the village Özlüce is situated on a plateau near the upper edge of the valley. Most of the species are concentrated on the slopes near Özlüce. Of another species composition is the butterfly fauna in the pass region (2600 m) already in the province Rize and from the pass downward to Sivrikaya and Dereköy on the northside of the pontic mountain with several alpine Caucasian elements (especially of the genus *Erebia*). This part of the mountain on both sides of the road to Rize should be included into the nature reserve (squares FE59, FE49, FF40 in Appendix 2). Both sides of the pass have a different climate and therefore a different flora and fauna which makes this region a very interesting one under ecological and biogeographical aspects.

The valley on the southside of the pass does not need any management, if the present state will be maintained. The very productive meadows on the northside above Sivrikaya in the province Rize could be cut once a year in late summer. But the yaylası are problematical by too much cattle grazing on the slopes and the settlements of the herdsmen with their families especially if the places are repeatedly changed. That way of land use conducts to fertilizing and in consequence to a commutation in the plant composition of the meadows wherefrom the disappearance of the foodplants of rare butterfly species unevitably follows and finally the disappearance of the butterflies themselves.

Palandöken Dağları. Palandöken Dağları (about 3100 m NN) about 10 km south of Erzurum and traversed by the road from Erzurum to Tekman are mountains different to the Kopdağ and Ovit Geçidi in its natural outfit but also rich in structures. The species composition therefore is not the same but in diversity, number of endemisms and rare species also very high (see squares FE90, FE91 in Appendix 2). There are long- and short-grassy slopes, rocky and stony ones and, in the upper parts, erosion gullies and ridges with well developed thorn-cushion-formations. Most of the butterflies fly between 2200 and 2500 m NN, others only above that line. Threats go out to the butterflies from overgrazing and in the lower parts especially from recreation pressure (picnicing in summer and winter sports). Just in the surroundings of Kayak Tesisleri the number of butterflies 20 years ago was still plentiful, today it has obviously declined. It should be taken into consideration, if it is not possible to reconcile conservation of nature and justified recreation through a sensible planning and management in cooperation with the relevant sections of the University.

Aras valley. Between Karakurt (1510 m NN, province Kars) and Tuzluca (1075 m NN, province Iğdır) the river Aras has carved out a deep valley in volcanic layers and created a very impressive landscape. The valley is the area of lowest precipitation within Turkey. But the higher slopes of the numerous side-valleys and the erosion gullies profit from the melting covering of snow and allow a diverse shrub vegetation, whilst the herbaceous steppe vegetation on the ground of the valley already dies by the end of June from the lack of rain. These differences in short distances create a lot of differentiated habitats and allows for very high diversity of endemic and rare butterfly taxa (see square LK53, south of Akcay). Here is the only occurrence of *Lycaena phoenicurus*, *Satyrium hyrcanicum cyri*, *Plebeius christophi transcaucasicus* in Turkey, and the only locality of *Polyommatus aedon araxianus* at all (all Turk-Iranian faunal elements). As the area is almost uninhabited nothing stands in the way to declare the valley with its side-valleys as a nature reserve. However, care should be taken that grazing does not get out of control.

Region south of Lake Van. The provinces south of Lake Van (Bitlis, Van, Siirt, Şirnak and Hakkari) may be deamed as the treasure chamber of nature for Turkey. Plateaus between 2000 and 3000 m protruded by mountains up to 4135 m covered from eternal snow, deep ravines of streams tributary to Tigris and populated by a relatively very thin human population. Especially some high passes like Kuzgunkıran (LH04), Kurubaş (LH55), Güzeldere (MH02), Süvarihalil (LG34, LG44, LG45, LG58), Tanintanin (LG14, LG25, LG35) and the deep valleys and ravines are very rich in endemic taxa and rare plants and insects. Most of these squares are traversed by the routes from Bitlis to Van, from Çatak to Van, from Van to Yüksekova – Şemdinli, from Van to

Hakkari – Çukurca and from Şırnak to Hakkari which are the best explored. But without doubt there are many other places with a valuable flora and fauna, only these are not accessible. The whole region is predestined for a large National Park like the big ones in the United States of America. It would not even be needed to resettle the people as the small towns and villages could remain and some could be included in a comprising management plan for the whole region, which conserves the present state of nature and gives some of the people an occupation. The small irrigated fields in the surroundings of the settlements are valuable habitats for butterflies and therefore should be preserved but not enlarged. Grazing in defined limits and horse breeding could be carried on in the traditional way. A weak and controlled mountaineering tourism might be of interest to the population to raise their income. But the main aim should be to conserve the unique nature, flora and fauna of the whole region accompanied by scientific exploration and research work – after it has been pacified. Let us hope!

Acknowledgements. The author wishes to give his cordial thanks to Bernd Beermann, Münster, for computerizing the maps, Hans Duffels, Amsterdam, for fruitful discussions, Harry van Oorschot, Badhoevedoorp, for help and the data from his databank, and Hikmet Özbek, Erzurum, for the exact topography of some localities.

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Received: 15.10.2003
Revised: 11.02.2004
Accepted: 15.04.2004

Corresponding editor: D. Stüning

APPENDIX 1

List of butterfly taxa occurring in Turkey with the number of 10 km UTM squares in which they have been observed

Hesperiidae	
Pyrginae	
Erynnis Schrank, 1801	
tages tages (Linnaeus, 1758)	241
marloyi marloyi (Boisduval, [1834])	122
Carcharodus Hübner, [1819]	
alceae alceae (Esper, [1780])	302
lavatherae tauricus Reverdin, 1915	137
flocciferus (Zeller, 1847)	19
orientalis Reverdin, 1913	205
stauderi ambiguus (Verity, 1925)	27
Spialia Swinhoe [1912]	
phlomidis (Herrich-Schäffer, [1845])	102
osthelderi osthelderi (Pfeiffer, 1932)	3
orbifer (Hübner, [1823])	426
Muschampia Tutt [1906]	
proto aragonensis (De Sagarra, 1924)	22
proteides (Wagner, 1929)	68
poggei poggei (Lederer, 1858)	46
plurimacula (Christoph, 1893)	6
tessellum tessellum (Hübner, [1803])	87
tessellum nomas (Lederer, 1855)	66
tessellum tersa Evans, 1949	20
Pyrgus Hübner [1819]	
carthami carthami (Hübner, [1813])	1
sidae sidae (Esper, [1784])	184
malvae malvae (Linnaeus, 1758)	18
melotis melotis (Duponchel, [1834])	17
melotis ponticus (Reverdin, 1914)	189
melotis graecus (Oberthür, 1910).	5
serratulae major (Staudinger, 1878)	164
serratulae balcanicus (Warren, 1926)	1
cirsii (Rambur, [1839])	24
cinarae cinarae (Rambur, [1839]	38
armoricanus persicus (Reverdin, 1913)	154
aleus alveus (Hübner, [1803])	40
jupei (Alberti, 1967)	7
bolkariensis De Prins & v. d. Poorten, 1995	3
aladaghensis De Prins & v. d. Poorten, 1995	4
Heteropterinae	
Heteropterus Duméril 1806	
morpheus (Pallas, 1771)	3
Carterocephalus Lederer, 1852	
palaemon (Pallas, 1771)	1
Hesperiinae	
Eogenes Mabille, [1909]	
alcides alcides (Herrich-Schäffer, [1852])	19
lesliei elama Wiltshire, 1941	2
Thymelicus Hübner, [1819]	
lineola (Ochsenheimer, 1808)	236
sylvestris syriacus (Tutt, [1905])	387
novus (Reverdin, 1916)	36
acteon acteon (Rottemburg, 1775)	80
hyrax (Lederer, 1861)	49
Hesperia Fabricius, 1793	
comma pallida (Staudinger, 1901)	85
Ochlodes Scudder, 1872	
sylvanus (Esper, 1777)	157
Gegenes Hübner, [1819]	
pumilio (Hoffmansegg, 1804)	33
nostrodamus (Fabricius, 1793)	19
Pelopidas Walker, 1870	
thrax (Hübner, [1821])	23
Papilionidae	
Parnassiinae	
Zerynthia Ochsenheimer, 1816	
polyxena gracilis Schultz, 1908	17
cerisy cerisy (Godart, 1824)	193
cerisy ferdinandi Stichel, 1907	2
deyrollei (Oberthür, 1869)	240
caucasica (Lederer, 1864)	10
Archon Hübner, 1822	
apollinus apollinus (Herbst, 1798)	215
apollinus forsteri Koçak, 1977	1
apollinus thracicus (Buresch, 1915)	2
apollinaris (Staudinger, [1892])	29
Parnassius Latreille, 1804	
mnemosyne caucasica Verity, [1911]	52
mnemosyne sheljuzhkoi Bryk, 1914	36
mnemosyne nubilosus Christoph, 1873	39
nordmanni nordmanni [Ménétriés], [1850]	1
nordmanni thomai de Freina, 1980	3
apollo graslini Oberthür, 1891	73
apollo tirabzonus Sheljuzhko, 1924	13
Papilioninae	
Iphiclides Hübner, [1819]	
podalirius podalirius (Linnaeus, 1758)	387
Papilio Linnaeus, 1758	
machaon syriacus Eller, 1936	288
alexanor eitschbergeri Bollino & Sala, 1992	62
alexanor orientalis Romanoff, 1884	22
Pieridae	
Pierinae	
Anthocharis Boisduval et al., [1833]	
cardamines cardamines (Linnaeus, 1758)	289
cardamines phoenissa Kalchberg, 1895	25
damone eunomia (Freyer, 1851)	91
gruneri gruneri Herrich-Schäffer, [1851]	78
gruneri armeniaca Christoph, 1893	28
Zegris Boisduval 1836	
eupheme menestho (Ménétrés, 1832)	82
Euchloe Hübner, [1819]	
belemia belemia (Esper, [1800])	15
ausonia taurica Röber, [1907]	350
Elphinstonia Klots, 1930	
penia (Freyer, 1851)	30
Aporia Hübner, [1819]	

crataegi (Linnaeus, 1758)	382
Pieris Schrank, 1801	
brassicae brassicae (Linnaeus, 1758)	410
krueperi krueperi Staudinger, 1860	61
mannii hethaea Pfeiffer, 1931	141
rapae rapae (Linnaeus, 1758)	588
ergane detersa Verity, [1908]	198
napi pseudorapae Verity, [1908]	368
bryoniae turcica Eitschb. & Hesselbarth, 1977	28
bryoniae goergneri Eitschberger, 1986	2
bowdeni Eitschberger, [1984]	13
Pontia Fabricius, 1807	
callidice chrysidice (Herrich-Schäffer, [1844])	33
daplidice (Linnaeus, 1758)	2
edusa (Fabricius, 1777)	650
chloridice chloridice (Hübner, [1813])	106
Colotis Hübner, [1819]	
fausta fausta (Olivier, [1804])	12
Coliadinae	
Colias Fabricius in Illiger, 1807	
erate erate (Esper, [1805])	5
crocea (Fourcroy, 1785)	779
chlorocoma Christoph, 1888	24
aurorina aurorina Herrich-Schäffer, [1850]	90
caucasica caucasica Staudinger, 1871	6
thisoa thisoa Ménétriés, 1832	13
thisoa shakuhensis Sheljuzhko, 1935	6
hyale (Linnaeus, 1758)	15
alfacariensis Ribbe, 1905	255
Catopsilia Hübner, [1819]	
florella (Fabricius, 1775)	1
Gonepteryx Leach, [1815]	
rhamni rhamni (Linnaeus, 1758)	38
rhamni miljanowskii Nekrutenko, 1966	26
rhamni transiens Verity, 1913	147
rhamni kurdistana de Freina, 1990	25
farinosa farinosa (Zeller, 1847)	107
farinosa turcirana de Freina, 1983	130
cleopatra cleopatra (Linnaeus, 1767)	17
cleopatra taurica (Staudinger, 1881)	43
Dismorphiinae	
Leptidea Billberg, 1820	
sinapis sinapis (Linnaeus, 1758)	282
reali Reissinger, 1989	?
duponcheli lorkovici (Pfeiffer, 1932)	274
Lycaenidae	
Riodininae	
Hamearis Hübner, [1819]	
lucina (Linnaeus, 1758)	2
Lycaeninae	
Cigaritis Donzel, 1847	
acamas acamas (Klug, 1834)	18
cilissa Lederer, 1861	9
maxima Staudinger, 1901	25
Lycaena Fabricius in Illiger, 1807	
phlaeas phlaeas (Linnaeus, 1761)	494

dispar rutila (Werneburg, 1864)	5
virgaureae virgaureae (Linnaeus, 1758)	125
virgaureae aureomicans (Heyne, 1897)	8
ottomanus (Lefebvre, 1830)	18
tityrus tityrus (Poda, 1761)	268
alciphron melibaeus (Staudinger, 1878)	289
candens candens (Herrich.Schäffer, [1844])	65
*thersamon (*Esper, [1784])	351
lampon lampon (Lederer, 1870)	6
thetis thetis Klug, 1834	138
asabinus (Herrich-Schäffer, [1851])	115
ochimus ochimus (Herrich-Schäffer, [1851]	148
phoenicurus (Lederer, 1870)	3
euphratica Eckweiler, 1989	14
Thecla Fabricius, 1807	
betualae betulae (Linnaeus, 1758)	6
Neozephyrus Sibatani & Ito, 1942	
quercus quercus (Linnaeus, 1758)	79
Tomares Rambur, 1840	
nogelii nogelii (Herrich-Schäffer, [1851])	66
nogelii obscura (Rühl, [1893])	6
nesimachus (Oberthür, 1893)	68
callimachus (Eversmann, 1848)	9
romanovi romanovi (Christoph, 1882)	21
Callophrys Billberg, 1829	
rubi (Linnaeus, 1758)	238
chalybeitincta Sovinsky, 1905	3
mystaphia Miller, 1913	26
suaveola (Staudinger, 1881)	17
Satyrium Scudder, 1876	
w-album (Knoch, 1782)	18
spini (Fabricius, 1787)	222
marcidum marcidum (Riley, 1921)	15
marcidum mardinum van Oorschot et al. 1985	1
ilicis ilicis (Esper, [1779])	262
zabni van Oorschot & van den Brink	65
acaciae (Fabricius, 1787)	98
abdominalis (Gerhard, [1850])	196
myrtale armenum (Rebel, 1901)	26
ledereri ledereri (Boisduval, 1848)	60
hyrcanicum cyri (Nekrutenko, 1978)	9
Lampides Hübner, [1819]	
boeticus (Linnaeus, 1767)	245
Leptotes Scudder, 1876	
pirithous (Linnaeus, 1767)	74
Tarucus Moore, [1881]	
balkanicus (Freyer, [1843])	114
Zizeeria Chapman, 1910	
karsandra karsandra (Moore, 1865)	21
Cupido Schrank, 1801	
minimus minimus (Fuessly, 1775)	39
minimus albocilia van Oorschot et al., 1984	8
osiris (Meigen, [1829])	281
argiades (Pallas, 1771)	62
alcetas (Hoffmansegg, 1804)	20
decoloratus (Staudinger, 1886)	1

Celastrina Tutt, 1906	
argiolus argiolus (Linnaeus, 1758)	309
Pseudophilotes Beuret, 1958	
vicrama schiffermuelleri (Hemming, 1929)	252
bavius egea (Herrich-Schäffer, [1852])	85
bavius eitschbergeri Koçak, 1975	3
bavius vanicola Koçak, 1977	20
Scolitantides Hübner, [1819]	
orion orion (Pallas, 1771)	5
Glaucopsyche Scudder, 1872	
alexis alexis (Poda, 1761)	366
astraea astraea (Freyer, [1851[)	41
astraea eckweileri Koçak, 1979	4
Jolana Bethune-Baker, 1914	
iolas lessei (Bernardi, 1964)	65
Maculinea van Eecke, 1915	
alcon monticola (Staudinger, 1901)	35
arion arion (Linnaeus, 1758)	39
nausithous (Bergsträsser, 1779)	17
Lachides Nekrutenko, 1984	
galba (Lederer, 1855)	9
Turanana Bethune-Baker, 1916	
cytis kurdistana Eckweiler, 1984	5
endymion endymion (Gerhard, [1851])	147
Chilades Moore, [1881]	
trochylus trochylus (Freyer, 1844)	80
Plebeius Kluk, 1780	
pylaon sephirus (Frivaldszky, [1835])	320
pylaon turcmenicus (Forster,1936)	47
pylaon nichollae (Elwes, 1901)	1
argus aegidion (Meisner, 1818)	314
idas baldur (Hemming, 1934)	109
idas altarmenus (Forster, 1936)	5
christophi transcaucasicus (Rebel, 1901)	6
argyrognomon caspicus (Forster, 1936)	17
argyrognomon subspecies nova ?	3
alcedo (Christoph, 1877)	48
rosei (Eckweiler, 1989)	1
morgianus morgianus (Kirby, 1871)	2
loewii loewii (Zeller, 1847)	318
eurypilus eurypilus (Freyer, 1851)	315
pyrenaicus dardanus (Freyer, [1843]	23
eumedon eumedon (Esper, [1780])	53
eumedon aladaghensis (Koçak, 1979)	9
eumedon modestus (Nekrutenko, 1972)	16
agestis ([Denis & Schiffermüller], 1775)	488
artaxerxes macedonicus (Verity, 1936)	8
artaxerxes sheljuzhkoi (Obraztsov, 1935)	17
teberdinus nahizericus (Eckweiler, 1978)	2
hyacinthus (Herrich-Schäffer, [1847])	16
torulensis (Hesselbarth & Siepe, 1993)	1
isauricus isauricus (Staudinger, 1871)	13
isauricus dorsumstellae (Graves, 1923)	16
isauricus latimargo (Courvoisier, 1913)	12
anteros anteros (Freyer, [1838])	121
anteros crassipunctus (Christoph, 1893)	45
bassoni (Larsen, 1974)	1
Polyommatus Latreille, 1804	
semiargus bellis (Freyer, [1842])	243
semiargus antiochenus (Lederer, 1861)	19
coelestinus (Eversmann, 1843)	131
diana (Miller, 1913)	9
fatima (Eckweiler & Schurian, 1980)	14
escheri (Hübner, [1823])	†
dorylas dorylas ([Denis & Schiffermüller], 1775)	42
dorylas armenus (Staudinger, 1871)	21
amandus amandus (Schneider, 1792)	226
thersites (Cantener, [1835])	279
myrrha myrrha (Herrich-Schäffer, [1851])	16
myrrha hakkariensis (Koçak, 1977)	11
aedon myrrhinus (Staudinger, 1901)	66
aedon araxianus (Koçak, 1980)	1
cornelia (Gerhard, [1851])	175
eros yildizae Koçak, 1977	16
eros molleti Carbonell, [1994]	1
eroides eroides (Frivaldszky, 1835)	6
ciloicus de Freina & Witt, 1983	3
bollandi Dumont, 1998	1
icarus (Rottemburg, 1775)	822
buzulmavi Carbonell, [1992]	9
daphnis daphnis ([Denis & Schiffermüller], 1775)	7
daphnis versicolor (Heyne, [1895])	286
daphnis elamita (Le Cerf, 1913)	36
bellargus (Rottemburg, 1775)	340
syriacus burak (Koçak, 1992)	14
dezinus (de Freina & Witt, 1983)	3
ossmar olympicus (Lederer, 1852)	†
ossmar ossmar (Gerhard, [1851])	90
corydonius caucasicus (Lederer, 1870)	117
coridon coridon (Poda, 1761)	1
alcestis alcestis (Zerny, 1932)	78
alcestis karacetinae Lukhtanov & Dantchenko, 2002	1
interjectus (de Lesse, 1960) (stat. inc.)	5
demavendi (Pfeiffer, 1938)	41
ripartii (Freyer, 1830)	124
erivanensis (Forster, 1960)	16
admetus (Esper, 1783)	185
mithridates (Staudinger, 1878)	60
antidolus (Rebel, 1901)	18
kurdistanicus (Forster, 1961)	7
menalcas (Freyer, [1837])	145
hopfferi (Herrich-Schäffer, [1851])	80
poseidon poseidon (Herrich-Schäffer, [1851])	89
putnami Dantchenko & Lukhtanov, 2002	2
caeruleus caeruleus (Staudinger, 1871)	†
dama dama (Staudinger, 1892)	2
wagneri (Forster, 1956)	91
maraschi Forster, 1956 (stat. inc.)	?
cilicius cilicius Carbonell, 1998	2

cilicius bolkarensis Carbonell, 1998	4
firdussii (Forster, 1956)	66
artvinensis (Carbonell, 1997)	13
bilgini Dantchenko & Lukhtanov, 2002	3
actis (Herrich-Schäffer, [1851])	2
sigberti Olivier et al., 2000	25
pseudactis (Forster, 1960) (stat. inc.)	?
haigi Dantchrenko & Lukhtanov, 2002	4
sertavulensis (Koçak, 1979) (stat. inc.)	6
ernesti Eckweiler, 1989 (stat. inc.)	3
erzindjanensis Carbonell, 2002	1
altivagans altivagans (Forster, 1956)	13
damocles kanduli Dantchenko & Lukhtanov, 2002	1
lycius (Carbonell, 1996)	4
pierceae Lukhtanov & Dantchenko, 2002	1
elbursicus (Forster, 1956)	16
turcicolus (Koçak, 1977)	17
*ninae (*Forster, 1956)	39
aserbeidschanus (Forster, 1956)	9
guezelmavi Olivier et al., 1999	1
theresiae Schurian et al., 1992	1
carmon carmon (Herrich-Schäffer, [1851])	58
carmon munzuricus (Rose, 1978)	2
anticarmon (Koçak, 1983)	9
schuriani schuriani (Rose, 1978)	13
surakovi sekercioglui Dantschenko&Lukhtanov, 2002	3
huberti (Carbonell, 1993)	39
turcicus (Koçak, 1977)	37
cyaneus cyaneus (Staudinger, 1890)	10
merhaba De Prins et. al., 1991	15
iphigenia iphigenia (Herrich-Schäffer, [1847])	84
iphicarmon Eckweiler & Rose, 1993	1
tankeri (de Lesse, 1960)	11
baytopi (de Lesse, 1959)	13
damon kotshubeji (Sovinsky, [1916])	30
phyllis vanensis (de Lesse, 1957)	36
Nymphalidae	
Libytheinae	
Libythea Fabricius in Illiger, 1807	
celtis (Laicharting, 1782)	100
Heliconiinae	
Argynnis Fabricius in Illiger, 1807	
paphia paphia (Linnaeus, 1758)	90
paphia delila Röber, 1896	14
pandora pandora ([Denis & Schiffermüller], 1775)	326
aglaja aglaja (Linnaeus, 1758)	117
aglaja ottomana Röber, 1896	23
adippe adippe ([Denis & Schiffermüller], 1775)	58
adippe taurica Staudinger, 1878	16
niobe orientalis Alphéraky, 1881	238
Issoria Hübner, [1819]	
lathonia (Linnaeus, 1758)	368
Brenthis Hübner, [1819]	

ino schmitzi Wagener, 1983	11
daphne daphne (Bergsträsser, 1780)	88
hecate hecate ([Denis & Schiffermüller], 1775)	8
hecate transcaucasica Wnukowsky, 1929	88
mofidii Wyatt, 1969	13
Boloria Moore, [1900]	
euphrosyne euphrosyne (Linnaeus, 1758)	55
dia (Linnaeus, 1767)	19
caucasica (Lederer, 1852)	13
graeca karina van Oorschot & Wagener, 1990	2
Nymphalinae	
Vanessa Fabricius in Illiger, 1807	
atalanta atalanta (Linnaeus, 1758)	161
cardui (Linnaeus, 1758)	630
Inachis Hübner, [1819]	
io io (Linnaeus, 1758)	53
Aglais Dalman, 1816	
urticae turcica (Staudinger, 1861)	197
Polygonia Hübner, [1819]	
c-album (Linnaeus, 1758)	93
egea (Cramer, [1775])	154
Araschnia Hübner, [1819]	
levana (Linnaeus, 1758)	1
Nymphalis Kluk, 1780	
vaualbum vaualbum ([Denis & Schiff.], 1775)	1
polychloros polychloros (Linnaeus, 1758)	106
xanthomelas fervescens (Stichel, [1908])	33
antiopa antiopa (Linnaeus, 1758)	61
Hypolimnas Hübner, [1819]	
misippus (Linnaeus, 1764)	1
Apaturinae	
Apatura Fabricius in Illiger, 1807	
ilia ([Denis & Schiffermüller], 1775)	1
metis metis Freyer, 1829	12
Euapatura Ebert, 1971	
mirza Ebert, 1971	19
Thaleropis Staudinger, 1871	
ionia (Eversmann, 1851)	75
Charaxinae	
Charaxes Ochsenheimer, 1816	
jasius jasius (Linnaeus, 1767)	16
Limenitidinae	
Limenitis Fabricius in Illiger, 1807	
camilla camilla (Linnaeus, 1764)	4
reducta herculeana Stichel, [1908]	241
Neptis Fabricius in Illiger, 1807	
rivularis rivularis (Scopoli, 1763)	8
Melitaeinae	
Euphydryas Scudder, 1872	
iduna inexspectata (Sheljuzhko, 1934)	1
orientalis (Herrich-Schäffer, [1845]	9
aurinia bulgarica (Fruhstorfer, 1917)	59
Melitaea Fabricius in Illiger, 1807	
cinxia cinxia (Linnaeus, 1758)	311
phoebe phoebe ([Denis & Schiffermüller], 1775)	119
punica telona Fruhstorfer, 1908	216

collina collina Lederer, 1861	34
collina lokmani van Oorschot & v. d. Brink, 1994	7
arduinna (Esper, [1783])	68
trivia trivia ([Denis & Schiffermüller], 1775	295
didyma didyma (Esper, [1778])	411
persea persea Kollar, 1849	91
interrupta interrupta Kolenati, 1846	32
diamina diamina (Lang, 1789)	11
aurelia ciscaucasica Rjabov, 1926	12
caucasogenita Verity, 1930	6
athalia athalia (Rottemburg 1775)	94
Danainae	
Danaus Kluk, 1780	
chrysippus chrysippus (Linnaeus, 1758)	15
Satyrinae	
Kirinia Moore, 1893	
roxelana (Kramer, [1777])	199
Esperarge Nekrutenko, 1988	
climene valentinae (Miller, 1923)	148
Pararge Hübner, [1819]	
aegeria aegeria (Linnaeus, 1758)	80
aegeria tircis (Godart, 1821)	76
Lasiommata Westwood, 1841	
megera transcaspica (Staudinger, 1901)	307
petropolitana petropolitana (Fabricius, 1787)	14
maera (Linnaeus, 1758)	290
menava Moore, 1865	4
Ypthima Hübner, 1818	
asterope asterope (Klug, 1832)	30
Coenonympha Hübner, [1819]	
arcania (Linnaeus, 1761)	66
glycerion glycerion (Borkhausen, 1788)	22
leander leander (Esper, [1784])	57
leander dierli Koçak, 1977	2
saadi mesopotamica Heyne, [1894]	107
symphyta Lederer, 1870	13
pamphilus (Linnaeus, 1758)	506
Triphysa Zeller, 1850	
phryne phryne (Pallas, 1771)	1
Pyronia Hübner, [1819]	
tithonus (Linnaeus, 1767)	23
cecilia (Vallantin, 1894)	1
Maniola Schrank, 1801	
jurtina (janira) phormia (Fruhstorfer, 1909)	436
megala (Oberthür, 1909)	18
telmessia (Zeller, 1847)	263
halicarnassus Thomson, 1990	6
Hyponephele Muschamp, 1915	
wagneri wagneri (Herrich-Schäffer, [1846]	70
urartua de Freina & Aussem, [1987]	8
naricina naricoides Groß, 1977	17
cadusia zerneca Skala, 2003	3
kocaki kocaki Eckweiler, 1978	4
kocaki melesina Weiss & Skala, 2000	5
lycaon ?collina (Röber, 1897) (stat. inc. nom. inc.)	206
?lycaon (?species nova, nom. inc.)	134
lycaon bugrai Koçak, 1989 (stat. inc.)	2
lycaon (Gürün-Form, stat. inc., nom. inc.)	8
lupina intermedia (Staudinger, 1886)	387
Proterebia Roos & Arnscheid, 1980	
afra afra (Fabricius , 1787)	35
Erebia Dalman, 1816	
aethiops aethiops (Esper, [1777])	16
aethiops melusina Herrich-Schäffer, [1847]	66
medusa euphrasia Fruhstorfer, 1917	33
hewitsonii Lederer, 1864	14
ottomana ottomana Herrich-Schäffer, [1847]	6
graucasica transcaucasica Warren, 1950	10
iranica dromulus Staudinger, 1901	†
melancholica Herrich-Schäffer, [1846]	11
Melanargia Meigen, 1828	
russiae russiae (Esper, [1783])	23
galathea satnia Fruhstorfer, 1917	108
syriaca syriaca (Oberthür, 1894)	14
syriaca kocaki Wagener, 1983	35
syriaca karabagi Koçak, 1976	33
hylata hylata (Ménétriés, 1832)	40
grumi Standfuss, 1892	60
titea titania Calberla,,1891	4
titea standfussi Wagener, 1983	38
titea wiskotti Röber, 1896	22
larissa lesbina Wagener, 1976	36
larissa astanda (Boisduval, 1848)	34
larissa noacki Wagener, 1983	231
larissa massageta Staudinger, 1901	11
larissa taurica Röber, 1896	105
Satyrus Latreille, 1810	
favonius favonius Staudinger, 1892	57
parthicus Lederer,1869	13
ferula (Fabricius, 1793)	23
amasinus amasinus Staudinger, 1861	69
amasinus iranicus Schwingenschuss, 1939	10
Minois Hübner, [1819]	
dryas dryas (Scopoli, 1763)	8
Hipparchia Fabricius in Illiger, 1807	
syriaca syriaca (Staudinger, 1871)	176
senthes (Fruhstorfer, 1908)	105
volgensis delattini Kudrna, 19775	3
pellucida pellucida (Stauder, 1924)	91
mersina (Staudinger, 1871)	86
statilinus (Hufnagel, 1766)	94
fatua fatua Freyer, [1843]	123
parisatis (Kollar, 1849)	46
Arethusana de Lesse, 1851	
arethusa ([Denis & Schiffermüller], 1775)	141
Brintesia Fruhstorfer, [1911]	
circe (Fabricius, 1775)	136
Chazara Moore, 1893	
briseis meridionalis (Staudinger, 1886)	373
persephone transiens (Zerny, 1932)	179
bischoffii (Herrich-Schäffer, [1846])	125
egina egina (Staudinger, 1892)	11

egina aisha Rose, 1986	3
Pseudochazara de Lesse, 1951	
beroe beroe (Freyer, 1843)	73
lydia lydia (Staudinger, 1878)	24
lydia obscura (Staudinger, 1878)	29
lydia aurora Eckweiler & Rose, [1989]	32
geyeri (Herrich-Schäffer, [1846])	92
mamurra mamurra (Herrich-Schäffer, [1846])	56
mamurra birgit Groß, 1978	30
mamurra schahrudensis (Staudinger, 1881)	13
schahkuhensis brandti (Holik, 1949)	1
pelopea persica (Christoph, 1877)	186
mniszechii mniszechii (Herrich-Schäffer, [1851])	154
mniszechii caucasica (Lederer, 1864)	31
mniszechii tisiphone Brown, 1980	1
anthelea anthelea (Hübner, [1824])	273
anthelea selcuki van Oorschot et al., 1987	8
thelephassa (Geyer, 1827)	81

The sign "†" with four taxa (*Polyommatus escheri*, *Polyommatus ossmar olympicus*, *Polyommatus caeruleus caeruleus*, *Erebia iranica dromulus*) symbolizes their extinction in Turkey, because they could no more be observed during the last fifty years. "?" for taxa whose taxonomic status and distribution is not fully understood.

Bonner zoologische Beiträge | Band 54 (2005) | Heft 1 | Seiten 25–95 | Bonn, April 2006

A Revision of Western Palaearctic *Medon*: the Species of the Atlantic Islands, the Western Mediterranean, and Europe, Except for the Southeast (Insecta: Coleoptera: Staphylinidae: Paederinae)

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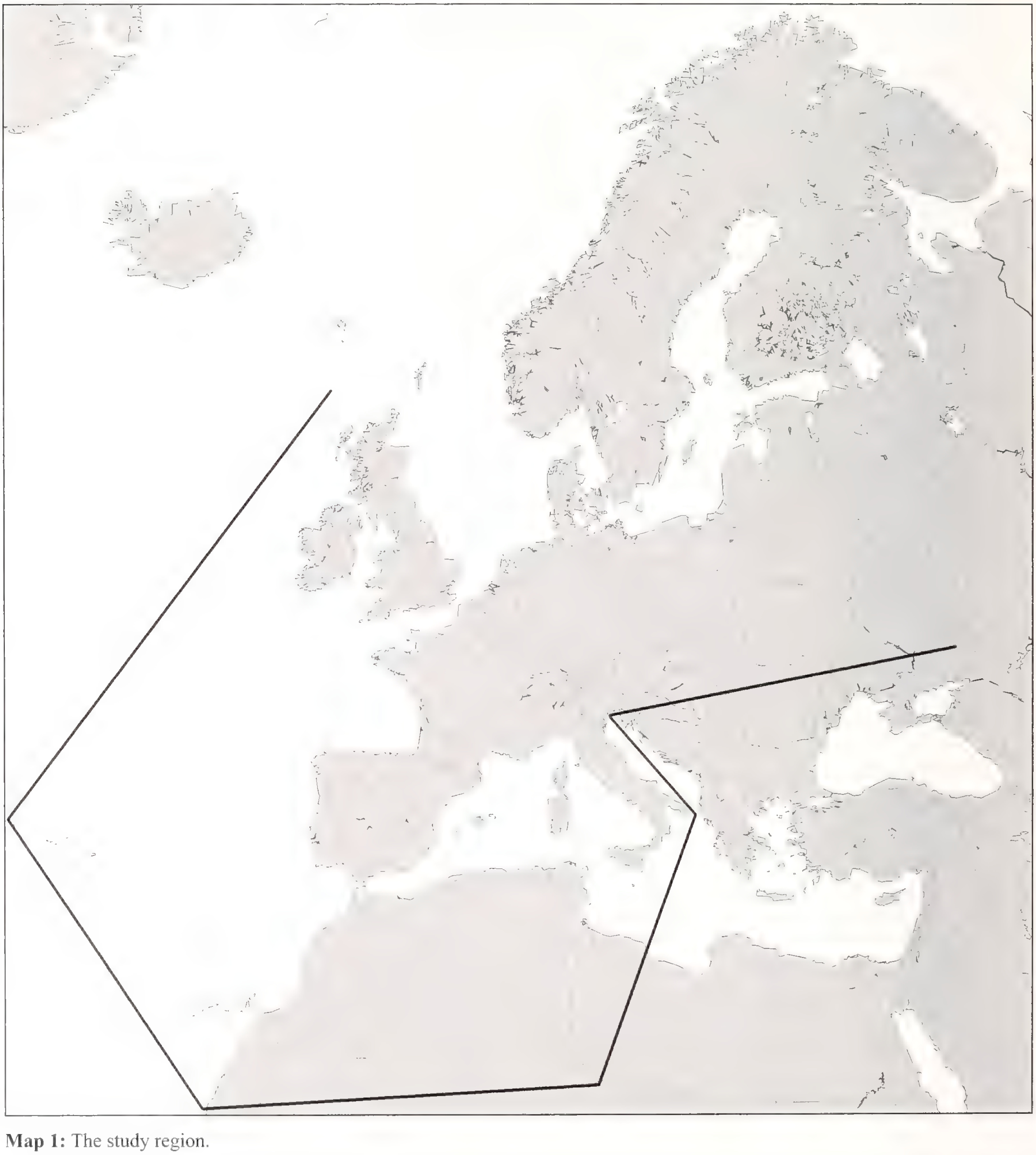
Abstract. Types and additional material of *Medon* Stephens are revised. 29 valid species and subspecies, including three doubtful species, are recognized in the region comprising the Western Mediterranean (including Italy and Tunisia), the Atlantic Islands, as well as Western, Central, and Northern Europe. *Medon oromii* **sp. n.** (Canary Islands: Gran Canaria), *M. antricola* **sp. n.** (Canary Islands: El Hierro), and *M. kabylicus* **sp. n.** (Algeria) are described. Twenty-three synonymies, two of them pertaining to the previously revised species of the Eastern Mediterranean region, are established: *Medon apicalis* (Kraatz, 1857) = *Medon orgianus* Bordoni, 1980 **syn. n.**; *Medon perniger* Coiffait, 1978 = *Medon perniger fraudulentus* Coiffait, 1978 **syn. n.**; *Medon dilutus* (Erichson, 1839) = *M. dilutus meridionalis* Bordoni, 1980 **syn. n.**; *M. dilutus cephalus* Koch, 1938 = *M. dilutus boeticus* Jeannel & Jarrige, 1949 **syn. n.**; *Medon dilutus quadriceps* (Wollaston, 1864) = *Medon vitalei* Bernhauer, 1936 **syn. n.** = *M. dilutus eremicus* Koch, 1939 **syn. n.** = *M. marocanus* Coiffait, 1970 **syn. n.** = *M. mateui* Coiffait, 1973 **syn. n.**; *Medon rufiventris* (Nordmann, 1837) = *M. burdigalensis* Coiffait, 1970 **syn. n.** = *M. aquitanicus* Coiffait, 1970 **syn. n.** = *M. siculus* Coiffait, 1970 **syn. n.** = *M. sicilianus* Coiffait, 1970 **syn. n.**; *Medon africanus* (Fauvel, 1872) = *M. bodemeyeri* Bernhauer, 1915 **syn. n.**; *Medon piceus* (Kraatz, 1858) = *M. murciensis* Coiffait, 1970 **syn. n.**; *Medon cauchoisi* Jarrige, 1949 = *M. oculatior* Peyerimhoff, 1949 **syn. n.** = *M. lusitanicus* Coiffait, 1970 **syn. n.** = *M. parviphallus* Coiffait, 1973 **syn. n.** = *M. mazices* Coiffait, 1973 **syn. n.** = *M. fongondi* Coiffait, 1980 **syn. n.** = *M. perraulti* Coiffait, 1980 **syn. n.**; *Medon mirei* Coiffait, 1980 = *M. giachinoi* Bordoni, 1988 **syn. n.**; *Medon semiobscurus* (Fauvel, 1875) = *M. ruber* Sahlberg, 1908 **syn. n.** = *M. sahlbergi* Scheerpeltz, 1933 **syn. n.** *Medon procerus* (Perez Arcas, 1874) and *M. sericellus* (Fairmaire, 1860), previously regarded as synonyms of *M. castaneus* (Gravenhorst, 1802) and *M. apicalis*, respectively, are revalidated. A neotype is designated for *Lithocharis sericella* Fairmaire, 1860. Lectotypes are designated for *Lithocharis oppidana* Kraatz, 1857, *L. picea* Kraatz, 1858, *Paederus castaneus* Gravenhorst, 1802, *Lithocharis africanus* Fauvel, 1872, *Medon bodemeyeri* Bernhauer, 1915, *M. bucharicus* Bernhauer, 1902, and *M. ruber* Sahlberg, 1908. *Medon pythonissa* (Saulcy, 1864) is regarded as a subspecies of *M. dilutus*. All the species not treated in the first part of the revision are described and illustrated. Bionomic and zoogeographic data are compiled, and the distributions of most species are mapped. A key to the *Medon* species of the Western Mediterranean region and the Atlantic Islands is provided. *Medon bucharicus* Bernhauer, 1902 (Middle Asia) is redescribed and moved to *Medon* again (from *Sunius* Curtis). Some additional records of species from other regions are presented. The previously published revision of Eastern Mediterranean *Medon* contains several errors, which are corrected in a separate section. These corrigenda include the following synonymies: *M. lydicus* Bordoni, 1980 = *M. mimulus* Fagel, 1970, **syn. n.** = *M. rhodicus* Franz, 1987, **syn. n.** = *M. choparti* Coiffait, 1987, **syn. n.**

Key words. Taxonomy, revision, new species, new synonyms, lectotype designations, neotype designation

1. INTRODUCTION

In the recently published first part of the revision of Western Palaearctic *Medon* and a subsequent supplement (ASSING 2004a, 2004b), the species of the Eastern Mediterranean and adjacent regions were treated. This project had been initiated especially by the difficulties encountered when trying to identify specimens from this area; attributing names to them was often little more than a good guess. This observation gave rise to the suspicion that many names were synonymous and/or misinterpreted, and, as was expected, one of the main results of this study was a significant reduction of the number of valid names.

For several reasons, the situation was hypothesized to be similar for the species of the Western Mediterranean. The species had never been thoroughly revised and numerous species have been described especially from France, the Iberian Peninsula, and from Northwest Africa. COIFFAIT (1984) lists 36 species and subspecies for the Western Mediterranean (including Italy, the Atlantic Islands, and Northwest Africa eastwards to Tunisia); three additional species were later described by SERRANO (1993), BORDONI (1988), and ASSING (1998). However, a preliminary examination of abundant material, which had been accumulated during various field trips in the past decades, suggested a significantly lower species diversity in this region. Many *Medon* species are inhabitants of the leaf litter and occur at relatively high densities, so that it seemed rather unlikely that a considerable number of species had just not been found. Moreover, the revision of the Eastern Mediterranean representatives of the genus had shown that the extent of the distributions and the range of intraspecific variation had generally been underestimated by previous authors. Also, some species, like *Medon burdigalensis* Coiffait and *M. aquitanicus* Coiffait, had never been recorded again after their description, although they had been described from regions where the presence of local endemics is unlikely; consequently, the absence of records could not be put down to extremely restricted distributions. These considerations, as well as the difficulty encountered when trying to identify *Medon* material from the study area suggested that the previous taxonomic concept of the *Medon* fauna of the Western Mediterranean was at least in part inadequate and eventually initiated the present revision.



Map 1: The study region.

The revision focuses on the species of the Atlantic islands and the western parts of the Mediterranean eastwards to Tunisia and Italy. However, since the ranges of several widespread species also extend into Western, Central, Northern, and even Eastern Europe, these regions are included, too (Map 1).

The recently published revision of Eastern Mediterranean *Medon* is based on an old manuscript version and contains some nomenclatural errors. I use the opportunity to correct them in a separate section at the end of this paper.

2. MATERIAL AND MEASUREMENTS

Types and additional material from the following institutions and private collections were examined:

DEI	Deutsches Entomologisches Institut, Eberswalde (L. Zerche)
DZUL	Departamento de Biología Animal – Zoología, Universidad de La Laguna (P. Oromí)
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Bruxelles (D. Drugmand)
FMNH	Field Museum of Natural History, Chicago (via L. H. Herman)
MCNT	Museo de Ciencias Naturales de Tenerife
MHNG	Muséum d´Histoire Naturelle, Genève (G. Cuccodoro)
MNHNP	Muséum National d´Histoire Naturelle, Paris (N. Berti)
MNHUB	Museum für Naturkunde der Humboldt-Universität, Berlin (J. Frisch, J. Willers)
MRSNT	Museo Regionale di Scienze Naturali, Torino (M. Daccordi)
NHMB	Naturhistorisches Museum Basel (E. Sprecher)
NHMW	Naturhistorisches Museum Wien (H. Schillhammer)
SMNS	Staatliches Museum für Naturkunde, Stuttgart (W. Schawaller, K. Wolf-Schwenninger)
UCBA	Università di Catania, Dip. di Biologia Animale (A. Adorno, G. Longo)
ZMH	Zoological Museum Helsinki (J. Muona)
cAss	author´s private collection
cBor	private collection A. Bordoni, Firenze
cErb	private collection D. Erber, Giessen
cEss	private collection J. Esser, Berlin
cFel	private collection B. Feldmann, Münster
cGil	private collection G. Gillerfors, Varberg
cGon	private collection A. Gontarenko, Odessa
cKap	private collection A. Kapp, Rankweil
cKöh	private collection F. Köhler, Bornheim
cOro	private collection P. Oromí, La Laguna
cOwe	private collection J. A. Owen, Epsom
cRou	private collection G. de Rougemont, Londinieres
cSch	private collection M. Schülke, Berlin
cTro	private collection M. Tronquet, Molitg-les-Bains
cWun	private collection P. Wunderle, Mönchengladbach
cZan	private collection A. Zanetti, Verona

Head length was measured from the anterior margin of the clypeus to the posterior margin of the head, elytral length along suture from the apex of the scutellum to the elytral hind margin.

3. THE *MEDON* FAUNA OF THE WESTERN MEDITERRANEAN

Based on an examination of 5600 specimens of *Medon*, including the accessible types, 26 valid species and subspecies are recognized, among them two revalidated and three previously undescribed species. The identities (and validity) of three additional species, *M. augur* Fauvel, *M. subterraneus* Coiffait, and *M. spelaeus* (Scriba), remain doubtful; *M. augur* is represented only by a female type specimen, and neither types nor non-type material of *M. subterraneus* and *M. spelaeus* were available. As expected, the true diversity of the *Medon* fauna in the Western Mediterranean was found to be distinctly lower than indicated by COIFFAIT (1984). Altogether 21 new synonymies were established for the *Medon* fauna of the study area. This enormous degree of synonymy – involving ten now valid species and subspecies, one of them with as many as six new synonyms – explains the difficulties previously encountered when trying to identify and interpret *Medon* species.

In the Western Mediterranean, as defined above, the genus is represented by at least four species groups. Since a phylogenetic analysis, which would require an inclusion also of Eastern Palaearctic species, has not yet been attempted, the species groups as outlined below must be considered tentative. The *Medon apicalis* group includes four species (*M. apicalis*, *M. perniger*, *M. sericellus*, *M. oromii*) and is characterized by a head with relatively ill-defined puncturation, more or less pronounced microculpture, and without distinct shine, a microsculptured pronotum with fine puncturation, rather long elytra, a male sternite VII with weakly modified marginal setae (no palisade setae), and either by an apically more or less incised or bifid ventral process (usual condition) or by an apically elongated apex (apomorphic in *M. oromii* and *M. sericellus*) of the aedeagus. In the Eastern Mediterranean and Middle Asia, this species group is represented by the widespread *M. maronitus* (Saulcy), by *M. beydaghensis* Fagel (southwestern Anatolia), and *M. bucharicus* Bernhauer (Middle Asia). The only Western Mediterranean species of the group whose range extends into the west of the Eastern Mediterranean is *M. apicalis*.

The species group previously referred to as the *M. ferrugineus* group (ASSING 2004a) is represented in the Western Mediterranean by ten species, all of which are characterized by more or less dilated protarsi (at least in the male), the presence of two combs of palisade setae at the posterior margin of the male sternite VII, by an angled (ventral view) or a more or less deeply incised (ventral view) apex of the aedeagus. This species group includes *Medon dilutus*, *M. subcoriaceus*, *M. antricola*, *M. castaneus*, *M. procerus*, *M. pocofer*, *M. rufiventris*, *M. africanus*, *M. vicentensis*, and *M. augur*. Of these species, only the distributions of *M. dilutus* (only the subspecies *M. dilutus pythonissa*), *M. pocofer*, and *M. rufiventris* extend into the Eastern Mediterranean region.

Five species of the *M. brunneus* group occur in the Western Mediterranean: *M. brunneus*, *M. piceus*, *M. cauchoisi*, *M. despectus*, and *M. mirei*. Only one of them, *M. brunneus*, also occurs in the Eastern Mediterranean. The species of this group are characterized by a usually well-defined puncturation of the head and pronotum, unmodified protarsi, the presence of two combs of palisade setae, and by an apically truncate or rounded, unincised aedeagus (ventral view).

The *M. fusculus* group, the species group with the highest diversity in the Eastern Mediterranean, is represented in the Western Mediterranean by only four species, the widespread Ponto-Mediterranean *M. fusculus*, the widespread Atlanto-Mediterranean *M. ripicola*, *M. sardous* from Sardinia, and *M. kabylicus* from Algeria. The systematic position of *M. ripicola* was previously unclear (ASSING, 2004a), but the respective character states in the evidently closely related *M. sardous* and *M. kabylicus* suggest that the distinctive morphology of the aedeagus represents a derived state of the condition usually found in the *M. fusculus* group and the absence of additional long marginal setae at the posterior margin of the male sternite VII is a secondary reduction. Consequently, *M. ripicola* is here attributed to the *M. fusculus* group. SERRANO (1993) erroneously attributed also *M. vicentensis* to this group, which is characterized especially by the shape and chaetotaxy of the male sternite VII, the broad semicircular excision of the male sternite VIII, as well as by the morphology of the aedeagus; for details see ASSING (2004a).

Two endemic species of the Atlantic Islands – *M. indigena* and *M. feloi* – may be monophyletic, both of them sharing the absence of palisade setae on the male sternite VII. This hypothesis would be supported also by a similar morphology of the aedeagus. Moreover, *Medon indigena* and *M. feloi* share a very similar shape of the male sternite VII, as well as a head and pronotum with sparse fine puncturation and with distinct microsculpture.

Eleven species have very restricted distributions. These include the endemics of the Canary Islands and Madeira – *M. indigena*, *M. subcoriaceus*, *M. antricola*, *M. vicentensis*, *M. feloi*, and possibly also *M. oromii* –, *M. sardous* from Sardinia, the microphthalmous *M. mirei* from northern Algeria, the troglobiont *M. procerus* from central Spain, possibly also *M. kabylicus* and *M. sericellus* from Algeria. The question whether or not *M. subterraneus*, *M. spelaeus*, and *M. augur* are valid endemic species will remain unanswered until material of these species becomes available for study and their taxonomic status is clarified. Of the remaining species, two are confined to Tunisia and Algeria: *M. africanus* and *M. despectus*, with the latter also occurring in the Italian island Pantelleria.

As was to be expected, most of the more widespread (sub-)species of the Western Mediterranean are Atlanto-Mediterranean elements sensu LATTIN (1967): *M. cauchoisi*, *M. ripicola*, *M. apicalis*, *M. ripicola*, *M. dilutus cephalus*, *M. piceus*, and *M. castaneus*. Three (sub-) species are Adriato-Mediterranean elements (*M. perniger*, *M. brunneus*, and *M. dilutus dilutus*), and two have a Ponto-Mediterranean distribution (*M. fusculus*, *M. rufiventris*). More data are needed to decide if *M. pocofer* represents an Atlanto- or an Adriato-Mediterranean element.

Ecologically, the *Medon* fauna of the study area is highly diverse. Several species – all the species of the *M. brunneus* group, plus *M. subcoriaceus*, *M. sardous*, *M. fusculus*, and *M. perniger* – apparently inhabit the litter layer and are only occasionally encountered also in other habitats; the same may be true of several other species, but too little is known about their ecology. Some species such as *M. castaneus* and *M. ripicola* are evidently associated with subterranean mammal nests. *Medon rufiventris* is usually found in or under dead wood, though its real habitat is unknown. Others – *M. procerus*, *M. feloi*, *M. antricola*, *M. vicentensis* – are doubtlessly troglobionts. The habitats of several species, among them the widespread *M. apicalis*, which is usually collected on the wing, are subterranean, but their exact nature is unknown.

Below, only those species that have not already been treated by ASSING (2004a) are redescribed and illustrated. Additional material of *Medon* species exclusively occurring in the region treated in the first part of the revision is compiled in a separate section at the end of the paper. In order to avoid redundancy, specimens already listed by ASSING (1998, 1999a, 2000, 2004a, 2004b) and ASSING & WUNDERLE (1999) are omitted from the material sections. In the references to the original descriptions, the original combination is given in the original spelling even when the gender of an adjectival name is incorrect (e. g. *Medon pernigrum* instead of *M. perniger*).

3.1. *Medon apicalis* (Kraatz, 1857) (Map 2)

Lithocharis apicalis Kraatz, 1857 (KRAATZ 1857: 715f).

Medon orgianum Bordoni, 1980 (BORDONI 1980: 83) **syn. n.**

Types examined: *L. apicalis*: see ASSING (2004a).

M. orgianus: Holotype ♂: ITALIA CENTR. To: Orgia (Si.) f. Merse, leg. Bordoni, IX.1974 / HOLOTYPUS / Medon orgianum n. sp. Det. A. Bordoni 1975 / Medon apicalis (Kraatz) det. V. Assing 2003 (cBor). Paratype ♀: mounted on same pin as holotype with extra label "Allotype ..." (cBor).

Comments: The holotype of *M. orgianus* is doubtlessly conspecific with *M. apicalis*. The synonymy of both names was independently recognized also by A. BORDONI (Firenze, pers. comm.) and A. ZANETTI (Verona, pers. comm.).

Additional material examined (total: 461 exs.; for additional material see ASSING (2004a)):

Morocco: 2 exs., Haut Atlas, NE Tizi-n-Test, 30°54N, 08°19W, 1710 m, edge of stream, 29.XII.2002, leg. Assing, Wunderle (cAss, cWun); 1 ex., NE Tizi-n-Test, 30°55N, 08°17W, 1150 m, 29.XII.2002, leg. Wunderle (cWun); 1 ex., 40 km N Oulmès, 27.II.1983, leg. Ledoux (cTro).

Portugal: 1 ex., Lisboa, Serra do Sintra, 24.V.1992, leg. Wunderle (cWun); 1 ex., Algarve, N Tavira, Alcaria do Cume, 37°15N, 07°44W, 440 m, 12.IV.2002, leg. Meybohm (cAss); 1 ex., Algarve, Serra de Monchique, NW Foia, 37°19N, 08°36W, 780 m, 15.IV.2002, leg. Meybohm (cAss); 3 exs., Algarve, Caldas de Monchique, V.-VI.1960, leg. Fagel (IRSNB). **Madeira:** 1 ex., Canico de Baixo, window, 20.-27.IX.1990, leg. Pieper (cAss); 5 exs., same data, but 7.-20.V.1992 (cAss); 1 ex., same data, but 14.-20.IX.1989 (cAss); 3 exs., Santo da Serra, 2.VIII.1975, leg. Vit (MHNG); 2 exs., Camacha, Lavada da Serra, 13.VIII.1975, leg. Vit (MHNG).

Spain: Galicia: 1 ex., Lugo, Sierra de Ancares, Tres Obispos, VI.1997 (cFel). **Asturias:** 12 exs., W Puerto de Pajares, Puerto de la Cubilla – Sotiello, 500 - 1400 m, car-net, 8.VI.1991, leg. Wunderle (cWun). **Cantabria:** 1 ex., Espinama, 27.VII.1972, leg. Lohse (cBor). **Cataluña:** 1 ex., Gerona, leg. Franz (NHMW); 1 ex., Gerona, Playa de Aro, 25.V.-5.VI.1971 (cBor); 12 exs., Seo de Urgel, Arfa, V.-VI.1962, leg.Fagel (IRSNB); 3 exs., Seo de Urgel, Sierra del Cadi, 1000 m, V.-VI.1962, leg. Fagel (IRSNB). **Aragón:** 1 ex., WNW Teruel, Sierra de Albarracín, NE Noguera, 40°30N, 01°35W, 1625 m, 11.IV.2003, leg. Assing (cAss). **Madrid:** 1 ex., Sierra de Guadarrama, El Escorial, leg. Franz (NHMW). **Valencia:** 10 exs., Alicante, Rio Sella, 25.III.1978 (cAss); 1 ex., Alicante, El Penon, leg. Franz (NHMW); 2 exs., Castellón, Cálig near Benicarlo, 6.V.1966, leg. Besuchet (MHNG). **Castilla-La Mancha:** 12 exs., SE Manzanares, Alhambra, 2.V.1925, leg. Scheerpeltz (NHMW); 1 ex., Albacete, Villaverde, 13.IV.1959, leg. Besuchet (MNHG). **Andalucía:** 1 ex., Sierra Nevada, Rio Genil, 37°08N, 03°24W, 1000 m, 24.II.2000, leg. Lompe (cAss); 2 exs., Sierra Nevada, Lanjaron, 26.IV.-18.V.1961, leg. Fagel (IRSNB); 1 ex., Puerto de Galis, 36°32N, 05°38W, 400 m, 20.II.2000, leg. Meybohm (cAss); 1 ex., Granada, Cenes near Granada, 24.V.1966, leg. Besuchet (MHNG); 1 ex., Algeciras env., Rio Guadarranque, 36°15N, 05°26W, flood plain forest, 21.II.2000, leg. Meybohm (cAss); 1 ex., Algeciras env., Sierra de Luna, 350 m, 28.III.1994, leg. Assing (cAss); 6 exs., Algeciras env., Sierra de Fates, 350 m, 28.III.1994, leg. Assing, Wunderle (cAss, cWun); 2 exs., Sierra de Bermeja (CA), Jubrique, 500 m, 26.III.1994, leg. Assing, Wunderle (cAss, cWun); 1 ex., Sierra de Bermeja (MA), Puerto de Peñas Blancas, 1200 m, 26.III.1994, leg. Wunderle (cWun); 1 ex., Cerro de la Novia, barranco at km 6 A-375, 36°37N, 05°30W, 700 m, 19.II.2000, leg. Lompe (cAss); 1 ex., Algeciras, Cerro de Mirador, leg. Franz (NHMW); 1 ex., Vejer de la Frontera (CA), 27.III.1987, leg. Zoia (cZan); 2 exs., Cordoba, Villaviciosa, 29.VI.1969, leg. Comellini (MHNG); 1 ex., Andújar, V.1959, leg. Comellini (cAss); 1 ex., E Jaén, SE Mancha Real, Sierra Almadén, ca. 37°45N, 03°33W, 1450-1850 m, *Q. ilex* litter, 26.XII.2003, leg. Assing (cAss). **Baleares:** 2 exs., Ibiza, Sierra Grosa, leg. Franz (NHMW, cAss); 1 ex., Ibiza, locality not specified, leg. Franz (NHMW). **Islas Canarias: Gran Canaria:** 1 ex., Bco. de la Miña, 1200 m, 21.XII.1997, leg. Assing (cAss); 1 ex., Bco. de la Virgen, 500 m, 20.XII.1997, leg. Wunderle (cWun); 2 exs., N Teror, Osorio, 600 m, 20.XII.1997, leg. Wunderle (cWun). **Tenerife:** 3 exs., Teno, Las Portelas, 700 m, 30.XI.1996, leg. Schülke (cSch, cAss).

France: Aquitaine: 1 ex., Landes, Saint-Sever-sur-l´Adour, 11.IX.1915 (cSch); 1 ex., Gironde, Léognan, VIII.1943, leg. Tempère (MHNG); 8 exs., Cap-Ferret, 17.IX.1928, leg. Tempère (MHNG); 4 exs., Gironde, Cambes, 17.III.1939, leg. Tempère (MHNG); 4 exs., Cambes, 10.IV.1939, leg. Giraud (MHNG); 1 ex., Gironde, Pessac, 5.VI.1928, leg. Tempère (MHNG). **Midi-Pyrénées:** 1 ex., Ariège, Foix, 3.IV.1953, leg. Tempère (MHNG); 4 exs., Hautes-Pyrenées, locality not specified, leg. Pandellé (NHMW). **Picardie:** 1 ex., Laigneville (Oise), VII.1908 (MHNG). **Île-de-France:** 2 exs., Cheptainville, 5.VIII.1945, leg. Levasseur (MHNG). **Centre:** 1 ex., Orléans (cBor); 1 ex., Perrusson, V.1905, leg. Mequignon (MHNG); 8 exs., Perrusson, XII.1903 (MHNG); 1 ex., same data, but III.1906 (MHNG); 11 exs., Perrusson, leg. Mequignon (MHNG); 2 exs., Loches (MHNG). **Rhône-Alpes:** 1 ex., Vaugneray (MHNG). **Provence:** 9 exs., Var, Tanneron, Auribeaux – Lac de S. Cassien, car-net, 30.-31.V.1991, leg. Wunderle (cWun); 1 ex., Var, Tanneron, car-net, VI.1988, leg. Wunderle (cWun); 5 exs., Var, Plan du Var [43°52N, 7°12E] (MHNG); 4 exs., Plan du Var, I.1954 (MHNG); 1 ex. [teneral], Ollioules, 15.X.1973 (MHNG); 1 ex., Var inundation (W Nice), III.1951 (MHNG); 1 ex., Alpes Maritimes, Sophia Antipolis near Antibes, haystack, 16.X.1991, leg. Schülke (cSch); 1 ex., Alpes Maritimes, Breil-sur-Roya, 1.VI.1955 (MHNG); 1 ex., Alpes Maritimes, "Gr. Dozol", X.1937 (MHNG); 1 ex., Alpes Maritimes, St.-Vallier-de-Thiey, V.1975, leg. Toumayeff (MHNG); 4 exs., Var, Bras, IV.1971, leg. Tronquet (cTro); 7 exs., Var, Gonfaron, chestnut litter, IV.1971, leg. Tronquet (cTro); 1 ex., Var, Vésubie inundation [near Lantosque], V.1961 (MHNG); 4 exs., Vaucluse, Mont Ventoux, 17.VI.1977, leg. Tronquet (cTro). **Corsica:** 1 ex., SE Corte, 200 - 900 m, car-net, 8.IV.1990, leg. Assing (cAss); 3 exs., Cursegliente-Pietroserana-Corte, 8.IV.1990, leg. Wunderle (cWun); 1 ex., Erbajolo-Bastinaco-Curtisi, car-net, 12.IV.1990, leg. Wunderle (cWun); 1 ex., Valle di Restonica, 800 - 1000 m, 6.-13.IV.1990, leg. Wunderle (cWun); 2 exs., NW St. Florent, Désert des Agriates, car-net, 21.IV.2001, leg. Zanetti (cZan); 1 ex., Casta, Campu Castingu, 300m, 18.VII.1976, leg. Sette (cZan); 1 ex., San Nicolao, 270 m, leaf litter, 18.VII.1994, leg. Zerche (DEI); 4 exs., Porto Vecchio, caught flying, V.1971, leg. Tronquet (cTro); 12 exs., Bocognano, caught flying, 28.V.1972, leg. Tronquet (cTro); 1 ex., Bocognano, caught flying, 26.V.1987, leg. Tronquet (cTro); 1 ex., Bocognano, 1905, leg. Leonhard (DEI); 2 exs., Cateraggio, caught flying, 1.VI.1987, leg. Tronquet (cTro); 1 ex., Francardo, VII.1954 (MHNG); 1 ex., Porto, V.1966 (MHNG); 1 ex., E Col de Vergio, Ft. Valdo-Niello [42°17N, 08°54E], caught flying, 25.V.1972, leg. Tronquet (cTro); 2 exs., locality not specified (DEI). **Locality ambiguous or not specified:** 1 ex., Prunelli, V.1960 (MHNG); 1 ex., "France", leg. Mulsant (MHNG).

England: 1 ex., Norwich, Norfolk, reed litter, 12.IV.1989, leg. Owen (cOwe).

Sweden: Gotland: 1 ex., Mästerby, 21.VI.1965, leg. Gillerfors (cGil); 1 ex., Vall, 8.VIII.1976, leg. Gillerfors (cGil); 3 exs., Buttle, 7.VIII.1976, leg. Gillerfors (cGil); 4 exs., Fide, 1.VIII.1975, leg. Gillerfors (cGil). **Skåne:** 4 exs., Stenshuvud, 19.III.1977, leg. Gillerfors (cGil). **Jämtland:** 1 ex., Svenstavik, 22.VI.1989, leg. Gillerfors (cGil). **Halland:** 1 ex., Hunnestad, 5.V.1978, leg. Gillerfors (cGil); 2 exs., Hunnestad, 4.VI.1988, leg. Gillerfors (cGil); 1 ex., Dagsås, 6.VI.1971, leg. Gillerfors (cGil); 1 ex., Dagsås, 9.IX.1977, leg. Gillerfors (cGil); 2 exs., Dagsås, 1.VI.1979, leg. Gillerfors (cGil). **Småland:** 1 ex., Ruggstorp, 11.VIII.1978, leg. Gillerfors (Gil). **Pite Lappmark:** 3 exs., Moskosel, 13.VI.1976, leg. Gillerfors (cGil). **Lule Lappmark:** 1 ex., Messaure, 23.VII.1978, leg. Gillerfors (cGil).

Germany: Nordrhein-Westfalen: 1 ex., Kreis Steinfurt, NSG Heiliges Meer, car-net, 8.V.1998, leg. Feldmann (cFel); 1 ex., Kreis Steinfurt, NSG Emsdettener Venn, car-net, 7.VI.1996, leg. Terlutter (cFel); 2 exs., Brüggen, Holter Heide, car-net, 19.VI.1995, leg. Wunderle (cWun); 3 exs., Düren, Gürzenich-Schevenhütte, car-net, 26.V.1989, leg. Wunderle (cWun); 3 exs., Jülich, Hambach, Lindenberger Wald, 2.VII.1991, leg. Köhler (cKöh); 4 exs., Bonn, Röttgen, Kottenforst, 3.VII.1991, leg. Köhler (cKöh); 2 exs., Brühl, Staatsforst Ville, 30.IV.1991, leg. Köhler (cKöh); 2 exs., Eifel, Gemünd, Der Kermeter, 6.V.1990, leg. Köhler (cKöh). **Rheinland-Pfalz:** 2 exs., Ulmen-Vollmerath, car-net, 9.VI.1983, leg. Wunderle (cWun); 1 ex., Staudernheim, 24.I.1995, leg. Köhler (cKöh); 2 exs., Monzingen, 18.-19.V.1991, leg. Köhler (cKöh); 1 ex., Schaidt, Bienwald, NWR Stuttpferch, 30.V.1996, leg. Köhler (cKöh); 2 exs., Bacharach, Steeg, 5.VI.1991, leg. Köhler (cKöh); 2 exs., Schloßböckelheim, 31.V.1996, leg. Köhler (cKöh); 1 ex., Taben/Saar, car-net, 6.-8.VI.1996, leg. Köhler (cKöh). **Schleswig-Holstein:** 1 ex., Eutin, 1.VI.1982, leg. Lohse (MHNG); 1 ex., Eutin, 1.VIII.1984, leg. Lohse (MHNG); 1 ex., Tensfeld, leg. Lohse (MHNG); 1 ex., Güster, 24.V.1958, leg. Lohse (MHNG); 1 ex., Güster, 7.VII.1977, leg. Lohse (MHNG); 2 exs." Farchau" (?), 13.V.1981, leg. Lohse (MHNG); 1 ex., Hornbek, 21.VI.1979, leg. Lohse (MHNG); 1 ex., Koberg, 14.V.1979, leg. Lohse (MHNG); 6 exs., Sachsenwald, 23.VI.1977, leg. Lohse (MHNG); 2 exs., Sachsenwald, 30.VII.1961, leg. Lohse (MHNG). **Hamburg:** 1 ex., Ohlstedt, 3.VI.1961, leg. Lohse (MHNG). **Niedersachsen:** 1 ex., Neustadt/Rbg., Himmelreich, window trap, 7.VII.1989, leg. Schmidt (cAss); 5 exs., Hannover, Eilenriede, car-net, 28.-29.V.1991, leg. Assing (cAss); 1 ex., same data, but 8.VII.1991 (cAss); 1 ex., Lüneburger Heide, Schneverdingen, Tütsberg, pitfall trap, 17.VI.1997 (cAss); 2 exs., Kreis Lüneburg, Amt Neuhaus/Elbe, car-net, 6.VII.1995, leg. Renner (cFel); 5 exs., Lüchow-Dannenberg, car-net, 1.VI.1983, leg. Renner (cWun); 1 ex., Lüchow-Dannenberg, Gar-tower Forst, 13.VI.1987, leg. Wunderle (cWun); 1 ex., Göhrde, 15.V.1983, leg. Lohse (MHNG); 4 exs., Göhrde, 8.VI.1977, leg. Lohse (MHNG); 2 ex., Göhrde, 21.V.1981, leg. Lohse (MHNG); 4 exs., Forst Göhrde, 1.VI.1983, leg. Lohse (MHNG); 4 exs., Forst Göhrde, 26.VII.1980, leg. Lohse (MHNG); 8 exs., Forst Göhrde, 6.VI.1980, leg. Lohse (MHNG); 1 ex., Wirl near Gartow, 6.VII.1983, leg. Lohse (MHNG); 1 ex., Lüchow-Dannenberg, Höhbeck, 1.V.1978, leg. Lohse (MHNG); 1 ex., same data, but 26.V.1979, leg. Lohse (MHNG); 1 ex., Lüchow-Dannenberg (cKöh); 2 ex., Uelzen, Brambostel, 2.VI.1991, leg. Lohse (MHNG). **Hessen:** 2 exs., Vogelsberg, Ehringhausen, car-net, V.1987, leg. Wunderle (cWun); 1 ex., Dautphe-Buchenau, Katzenbachtal, car-net, 26.IV.1987, leg. Wunderle (cAss). **Berlin/Brandenburg:** 19 exs., Berlin, Hohen Neuendorf (DEI). **Sachsen:** 3 exs., Guttau, car-net, 25.V.1985, leg. Schülke & Heinig (cSch); 3 exs., Oberlausitz, Daubitz, haystack, 23.IV.1994, leg. Schülke (cSch, cAss); 1 ex., Weißwasser, car-net, 17.V.1984, leg. Apel (DEI).

Austria: Niederösterreich/Wien: 11 exs., several localities in the surroundings of Wien (NHMW); 7 exs., Wienerwald, Hadersdorf, leg. Skalitzky (MHNG, NHMW); 5 exs., Wien, Pötzleinsdorfer Park (MHNG). **Kärnten:** 1 ex., Gurktaler Alpen, Falkert, car-net, 24.VII.1991, leg. Assing (cAss); 4 exs., Eisenkappel, car-net, 26.VI.-4.VII.1987, leg. Siede & Wunderle (cWun). **Steiermark:** 1 ex., Pleschkogel near Rein, 590 m, sifted forest litter, 20.VI.1995, leg. Zerche & Behne (DEI).

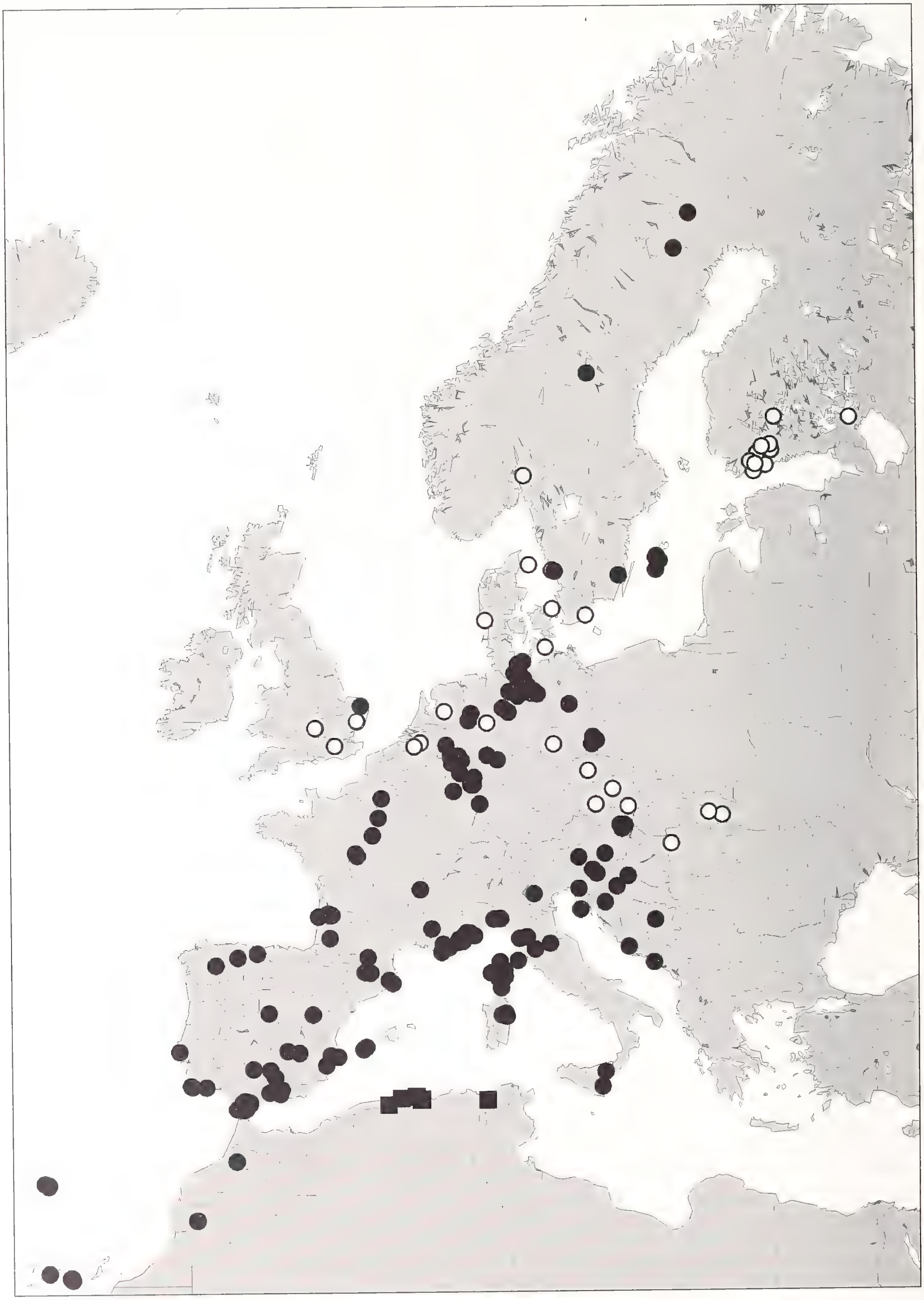
Italy: Liguria: 1 ex., San Remo, leg. Schneider (DEI); 2 exs., Genova, Premanico, 17.XII.1972, leg. Bartoli (UCBA); 2 exs., Casanova di St. Olcese (GE), 26.III.1972, leg. Bartoni (UCBA). **Friuli-Venezia Giulia:** 1 ex., Rupin Grande (TS), car-net, 15.V.1994, leg. Zanetti (cZan). **Veneto:** 1 ex., Tregnago – Vestenavecchia, car-net, 20.IV.1996, leg. Zanetti (cZan). **Toscana:** 8 exs., E Arezzo, Lippiano near Padonchia, XI.1924, leg. Andreini (UCBA, cBor); 1 ex., San Rossore (Pisa), 30.I.1969, leg. Santini (cBor); 1 ex., Padule di Fuccechio, leg. Castellini (cTro). **Elba:** 3 exs., leg. Paganetti (DEI, cAss). **Sardegna:** 1 ex., NE Lula (NU), 600 m, 23.IV.1992, leg. Scheuern (cWun); 1 ex., NE Lula, 600 m, 23.IV.1992, leg. Schawaller (cSch); 1 ex., 10 km NNW Nuoro, Grotta Cuccu, Monte Tiria, 27.VIII.1994 (cBor); 3 exs., 5 km SW Galtelli (NU), light source, 16.VII.1999, leg. Zanetti (cZan); 1 ex., Galtelli, car-net, 17.VII.1999, leg. Zanetti (cZan); 1 ex., locality not specified (DEI). **Sicilia:** 1 ex., M. Iblei, Cava Gissara, Melilli (SR), 300 m, 6.VI.1991, leg. Sabella (UCBA); 2 exs.,Taormina (ME), Isola Bella, 8.X.2002 (UCBA); 4 exs. same locality, 7.XI.2002 (UCBA, cAss).

Slovenia: 1 ex., Savina, leg. Paganetti (MHNG).

Locality not indicated: 3 exs. (MHNG).

Diagnosis: See ASSING (2004a) and the key in section 4.

Distribution and bionomics: *Medon apicalis* is widespread in the western parts of the Western Palaearctic region (Map 2). It occurs in the Canaries (Tenerife and Gran Canaria), Madeira, and Morocco; in continental Europe, its distribution ranges from the Iberian Peninsula in the southwest to England and Scandinavia in the north, and to the northern Balkans in the southeast (material examined). It has also been reported from the Azores (BERNHAUER 1940; GILLERFORS 1988; LUNDBLAD 1958; SMETANA 1970). In Scandinavia it is the most widespread and least rare species of the genus; in Sweden it has been recorded as far north as Lule Lappmark and Norrbotten (material examined; LUNDBERG 1995). *Medon apicalis* is, however, unknown from the Baltic countries (SILFVERBERG 1992). In the British Isles, only few localities are known from southern England (FOWLER 1888; JOY 1932). NORMAND (1935) records *M. apicalis* also from Tunisia, but these records may refer to similar species (*M. ripicola*, *M. kabylicus*, *M. sericellus*); I have seen no material from there. For a selection of additional literature records see BOHÁČ (1985), BRUGE et al. (2001), DRUGMAND (1989), FOWLER (1888), M. HANSEN (1996), HANSEN et al. (1994, 1995), V. HANSEN (1964), HORION (1965), HUGENTHOBLER (1966), KOCH (1968), KÖHLER (2000), KÖHLER & KLAUSNITZER (1998), LUNDBERG (1995), SILFVERBERG (1992), TERLUTTER (1995), and TRONQUET (2001). In the southern Balkans, Anatolia, and the Caucasus region, *M. apicalis* is replaced by *M. maronitus* (Saulcy) (ASSING 2004a). In Italy, where the closely related *M. perniger* is much more abundant, *M. apicalis* has been found in the north, in Toscana, and in the islands Elba, Sardegna, and Sicilia. In some Italian localities and in the Alpes Maritimes, *M. apicalis* and *M. perniger* were apparently collected together: Toscana (Lippiano, San Rossore), Liguria (Premanico, Casanova di St. Olcese (GE)), Sicilia (Isola Bella), Alpes Maritimes (Antibes). All previous literature records of *M. apicalis* from Italy must be considered doubtful due to probable confusion with *M. perniger*.



Map 2: Distributions of *Medon apicalis* (Kraatz) (filled circles: revised records; open circles: selected unexamined records) and *M. sericellus* (Fairmaire) (filled squares, examined records).

The species has been collected in various biotopes and habitats. In the material examined, the vast majority of specimens collected in spring and early summer (April through July) were taken on the wing (mostly by car-net, but also by flight interception traps). Ilpo RUTANEN (Hyvinkää, pers. comm. 2003) communicated to me 22 records from southern Finland, 21 of which were made with a car-net (June through August). The remainder of the specimens examined were found in various types of woodland, at the edge of streams, under haystacks, or at light sources. Some of the records from early spring are apparently from flood debris. The reproduction habitat of *M. apicalis* is cryptic and unknown. According to HORION (1965) and KOCH (1968), the species is possibly associated with nests and burrows of voles and mice. NOWOSAD (2000), however, examined 7000 nests of various small mammals and birds, but found *M. apicalis* only occasionally. All the records of *M. apicalis* from mole nests by OSELLA & ZANETTI (1974) refer to *M. perniger*. Adult beetles have been recorded throughout the year; teneral specimens were observed in autumn (October). DRUGMAND (1989) states that the species is bivoltine, but there is no evidence supporting this. Based on the material examined here, *M. apicalis* is univoltine.

3.2. *Medon perniger* Coiffait, 1978 (Figs. 1-7, Map 3)

Medon apicalis var. *pernigrum* Coiffait, 1970a (COIFFAIT 1970a: 717); unavailable name (infrasubspecific).

Medon pernigrum Coiffait, 1978 (COIFFAIT 1978: 268f).

Medon pernigrum fraudulentum Coiffait, 1978 (COIFFAIT 1978: 269f) **syn. n.**

Types examined: *M. perniger*: Holotype ♂: Emilie, Parme / MUSEUM PARIS COLL H. COIFFAIT / HOLOTYPE / Medon pernigrum H. COIFFAIT 1963 / Holotypus Medon perniger Coiffait rev. V. Assing 2003 (MNHNP).

M. perniger fraudulentus: Paratype ♂: ♂ / Sicilien, Messina, April 43. / leg. Wolfrum / Medon apicalis det. E. Ulbrich 1966 / MUSEUM PARIS COLL H. COIFFAIT / PARATYPE / Edeage casse / Medon pernigrum fraudulentum H. COIFFAIT 1978 [?] / Medon perniger det. V. Assing 2003 (MNHNP).

Comments: The holotype of *M. perniger* is a relatively dark specimen. The main difference between *M. perniger* and *M. p. fraudulentus* indicated by COIFFAIT (1978) is the lighter coloration of the latter. This coloration, however, is clearly within the range of intraspecific variation throughout the range of the species. No significant differences could be found in the male sexual characters, so that *M. p. fraudulentus* is here placed in the synonymy of *M. perniger*.

Additional material examined (total: 298 exs.):

France: 1 ex., Alpes Maritimes, Sophia Antipolis near Antibes, haystack, 18.X.1991, leg. Schülke (cSch); 1 ex., Var, Argens inundation [43°27N, 06°30E], 17.I.1955 (MHNG); 1 ex., Var, Vésubie inundation [near Lantosque], V.1961 (MHNG); 1 ex., Alpes Maritimes, "St. Pons", VI.1956 (MHNG); 1 ex., Alpes Maritimes, Menton, inundation, V.1952 (MHNG).

Switzerland: 2 exs., Ticino, Locarno, VIII.1944 ["Typus Medon linderi O. Scheerpeltz"; manuscript name] (NHMW).

Italy: Trentino-Alto Adige: 1 ex., Trento, Villa Lagarina, 950 m, 29.IV.1962, leg. Petrolli (cBor). **Piemonte:** 2 exs., Cuneo, Colle San Bernardo, N Erli, 600 m, 12.X.1997, leg.Wolf (cSch); 1 ex., locality not specified, leg. Baudi (DEI). **Lombardia:** 1 ex., Alpi Orobi, Morbegno, 350 m, deciduous forest, 18.VIII.1994, leg. Assing (cAss); 1 ex., Zecchone near Pavia, 17.X.1977, leg. Kanaar (cSch); 2 exs., Rivolta d´Adda, 23.X.1959, leg. Rosa (NHMW, cAss); 1 ex., Ostiglia (MN), Palude del Busatello, 7.III.1982, leg. Zanetti (cZan); 10 exs., Mantova, Bosco Fontana, 27.I.1980 (5 exs.), 7.V.1989 (1 ex.), 11.VI.1989 (1 ex.), 12.X.1989 (3 exs.), leg. Zanetti (cZan); 1 ex., Torbiere d´Iseo (BS), 28.III.1982, leg. Zanetti (cZan); 4 exs., Castellaro Lagusello (MN), 2.XII.1990, leg. Zanetti (cZan); 1 ex., Pozzolo (MN), 1.IV.1990, leg. Zanetti (cZan); 1 ex., Oltre il Colle, 18.VII.1914 (DEI); 1 ex., Corana (PV), 12.IV.1970, leg. Briganti (UCBA); 1 ex., Bereguardo, 2.V.1943, leg. Paganetti (MHNG). **Veneto:** 1 ex., Arcole (VR), 12.III.1971, leg. Pace (cBor); 3 exs., Sona (VR), 1.III.1970, leg. Zanetti (cZan); 1 ex., Valli Grandi Veronesi, La Torretta [45°06N, 11°16E], leg. Zanetti (cZan); 14 exs., San Giovanni Lupatoto (VR), mole nests, 28.IX.1973, leg. Zanetti (cZan, cAss); 3 exs., same data, but 16.XI.1973 (UCBA, cZan); 1 ex., same locality, "base di *Salix*", 2.II.1975, leg. Zanetti (cZan); 4 exs., NW Villafranca di Verona, Custoza, mole nests, 10.II.1974, leg. Zanetti (cZan); 1 ex., Custoza, 24.XI.1974, leg. Zanetti (cZan); 1 ex., Bussolengo – Sommacampagna (VR), car-net, 24.VI.1989, leg. Zanetti (cZan); 2 exs., Verona, P.te Saval, 26.II.1974, leg. Zanetti (cZan); 3 exs., Montecchia di Crosara (VR), mole nest, 22.II.1976, leg. Zanetti (cZan); 2 exs., Soave – Montecchia d. C., car-net, 20.IV.1996, leg. Zanetti (cZan); 1 ex., San Martino Buon Albergo (VR), Musella Ferrazzetta, mole nest, 28.II.1991, leg. Zanetti (cZan); 1 ex., Pastrengo (VR), 20.IV.1984, leg. Zanetti (cZan); 1 ex., Pellegrina (VR), mole nest, 3.II.1980, leg. Zanetti (cZan); 1 ex., Tregnago (VR), 26.XII.1976, leg. Zanetti (cZan); 2 exs., Tregnago – Vestenavecchia, car-net, 20.IV.1996, leg. Zanetti (cZan); 1 ex., Negrar (VR), Montericco, light source, IV.2002, leg. Zanetti (cZan). **Emilia-Romagna:** 4 exs., Sant´Agostino (FE), Bosco

Panfilia, 20 m, nest of *Apodemus*, 23.III.1997, leg. Tagliapietra & Zanetti (cZan); 2 exs., Valle Scoltenna (N Sestola) (MO), car-net. 1.VI.1996, leg. Zanetti (cZan). **Friuli-Venezia Giulia:** 1 ex., Udine, Chiarpena, 200 m, 20.X.2001, leg. Kahlen (cAss). **Liguria:** 1 ex., ca. 30 km NW La Spezia, Zignago, VII.1962 (cBor); 3 exs., La Spezia, Le Grazie, 5.XII.1982, leg. Zoia (cZan); 5 exs., Genova, Ruta, leg. Dodero (NHMW, cAss); 1 ex., Genova, Premanico, 17.XII.1972, leg. Bartoli (UCBA); 1 ex., Neirone (GE), S. Marco d´Ursi, 30.XII.1982, leg. Zoia (cZan); 1 ex., Bordighera (DEI); 1 ex., La Spezia, Déiva Marina near Piazza, 5.IV.1970, leg. Briganti (UCBA); 2 ex., Graveglia (GE), Pian di Fieno, 19.III.1976, leg. Zoia (UCBA); 6 exs., Casanova di St. Olcese (GE), 18.IV.1973, leg. Bartoli (UCBA); 1 ex., same data, but 26.III.1972 (UCBA); 34 exs., Genova (città), Villetta Di Negra, 1.&8.X.1972, leg. Bartoli (UCBA); 2 exs., same data, but 7.V.1975 (UCBA); 1 ex., 10 km NE Genova, Creto, 2.V.1977, leg. Parodi (UCBA); 1 ex., Genova, V.1920, leg. Mancini (UCBA); 1 ex., Genova, leg. Natterer (MHNG); 3 exs., Arenzano (GE), 6.XI.1977, leg. Gardini (UCBA); 1 ex., Ameglia, IX.1913, leg. Mancini (UCBA). **Toscana:** 1 ex., Livorno, Tenuta di Tombola, 11.IV.1992, leg. Schawaller (SMNS); 1 ex., SW Firenze, Figline d´Arno, 200 m, 14.VI.1992, leg. Assing (cAss); 1 ex., Vallombrosa, Regelle, 750 m, 28.IV.1991, leg. Wunderle (cWun); 7 exs., Grassina (FI), 350 m, flood debris, 3.V.1991, leg. Wunderle (cWun, cAss); 2 exs., Mt. di Calvani (FI), Mungona, 650 m, 1.V.1991, leg. Wunderle (cWun); 1 ex., Cecina, 4.IX.1972, leg. Pace (cBor); 3 exs., San Rossore (PI), 22.&30.I.1969, leg. Santini (cBor); 2 exs., Tana Termini (?) (Lucca), VI.1930, leg. Andreini (cBor); 5 exs., Arezzo, inundation of Arno river, XI.1926, leg. Andreini (cBor, cAss); 1 ex., Arezzo, Palazzo del Pero, 9.IV.1961 (cBor); 5 exs., E Arezzo, Lippiano near Padonchia, XI.1924, leg. Andreini (UCBA, cBor); 4 exs., Firenze, 21.I.1962, leg. Castellini (cBor); 7 exs., 15 km ESE Massa, Volegno, V.1967, leg. Bordoni (cBor); 1 ex., Piteccio, 21.IV.1969, leg. Failla (cBor); 1 ex., N Borgo San Lorenzo, Grezzano, 27.X.1974, leg. Rocchi (cBor); 2 exs., Ponteginori (SI), 4.IV.1994, leg. Gardini (cZan); 1 ex., Uccellina, Collelungo [42°37N, 11°05E], light-source, 12.VI.1977, leg. Zanetti (cZan); 4 exs., Antona, IV.1911, leg. Mancini (UCBA); 1 ex., Rignano sull´Arno, V.1974, leg. Castellini (cTro). **Umbria:** 1 ex., Sigillo (PE), M. Cucco, 20.IV.1975, leg. Rossi (cZan). **Lazio:** 2 exs., Mte. Circeo, 300 - 450 m, *Quercus ilex* forest, 27.XII.1994, leg. Assing (cAss); 4 exs., Mte. Circeo, mixed forest, 29.XII.1994, leg. Assing (cAss); 1 ex., Itri, 400m, 25.IV.1977, leg. Zampetti (cZan). **Abruzzo:** 1 ex., Cappelle sul Tavo (PE), 13.VII.1974, leg. Zanetti (cZan); 1 ex., Fiume Sinello (CH), Bosco di Don Venanzo [41°55N, 14°26E], car-net, 23.VII.1998, leg. Zanetti (cZan); 1 ex., Maiella, Madonna della Mazza, 1020 m, 28.V.2003, leg. Kapp (cKap). **Puglia:** 1 ex., Gargano, Forest Umbra, 600 m, beech forest, 30.XII.1994, leg. Assing (cAss); 2 exs., Foresta Umbra (FG), 800m, 6.V.1982, leg. Angelini (cZan). **Campania:** 10 exs., Napoli, Sorrent, S. Agata su due Golfi, 40°37N, 14°23E, 430 m, chestnut forest, 12.V.2002, leg. Wunderle (cAss); 2 exs., 5 km NE Salerno, Mte. Stella, leg. Liebmann (cBor). **Basilicata:** 2 exs., Lucania, Nova Siri (MT), 500m, 29.IV.1979, leg. Angelini (cRou); 1 ex., E Lagonegro, Mt. Sirino, 40°06N, 15°51E, 7.V.2002, leg. Wunderle (cWun); 4 exs., Maratea, 40°01N, 15°44E, 485 m, 12.V.2002, leg. Wunderle (cWun); 1 ex., Rivello, 400 m, oak forest, 6.V.2002, leg. Wunderle (cWun); 1 ex., Taranto, Policoro near Scanzano/Jonico, 22.X.2000, leg. Wolf (cSch); 1 ex., Policoro (MT), 1.VII.1982, leg. Angelini (cZan). **Calabria:** 10 exs., Aspromonte, dint. San Luca, 300 m, 24.VI.1987, leg. Angelini (cAss); 1 ex., S. Eufemia d´Aspromonte, 31.VII.1975, leg. Pace (cBor); 1 ex., S. Eufemia, 10.VII.1997, leg. Adorno (UCBA); 2 exs., S. Eufemia, 31.VI.1993 (UCBA); 1 ex., S Cittanova, Zómaro, 12.VII.1988 (cZan); 2 exs., Antonimina, 1.VI.1993 (UCBA); 2 exs., Antonimina, mixed forest, 3.V.1993 (UCBA). **Sardegna:** 1 ex., Siniscola, light source, 19.IX.1987 (cAss); 2 exs., Salto di Quirra, 400 m, 9.X.1989, leg. Wunderle (cWun); 2 exs., Iglésias, Grotta del Torpedo (?), 18.XI.1970 (cBor). **Sicilia:** 8 exs., San Fratello, 750 m, oakwood, 30.VI.1978, leg. Pace (cZan, cAss); 2 exs., Lascari – Gratteri (PA), car-net, 7.VII.2000, leg. Zanetti (cZan); 1 ex., Noto Antica, 16.-17.VII.1991, leg. Zanetti (cZan); 1 ex., Macchia (CT) (UCBA); 1 ex., Aci Sant´Antonio (CT), 14.V.1992 (UCBA); 1 ex., Peloritani, Foresta di Ferra, Santa Lucia del Mela (ME), 570 m, 6.VI.1996, leg. Adorno (UCBA); 3 exs., Messina, leg. Vitale (UCBA); 3 exs., Messina, 6.III.1943 (NHMW); 1 ex., locality illegible, leg. Ragusa (UCBA); 1 ex., N Mongiuffi Melia, Límina, 14.V.1993 (UCBA); 1 ex., Gerace, Zomino, 15.XI.1993 (UCBA); 1 ex., Taormina (ME), Isola Bella, 8.X.2002 (UCBA); 3 exs., same locality, 7.XI.2002 (UCBA, cAss); 1 ex., M. Iblei, Cassaro (SR), bank of Anapo river, 5.III.1997 (UCBA); 1 ex., Buccheri (SR), Bosco di Accoro, Valle Cupa, 1.XI.1996 (UCBA).

Locality doubtful, illegible, or not indicated: 4 exs., "Alta Valle Tosco-Umbra", inundation of Tevere river, 18.XI.1935, leg. Andreini (cBor); 1 ex., leg. Parodi (UCBA); 2 exs., without locality (UCBA); 2 exs. [confusion of locality labels?], Turkmenistan, Loṭfābād ["Ljutfabad"] (MNHUB, cAss).

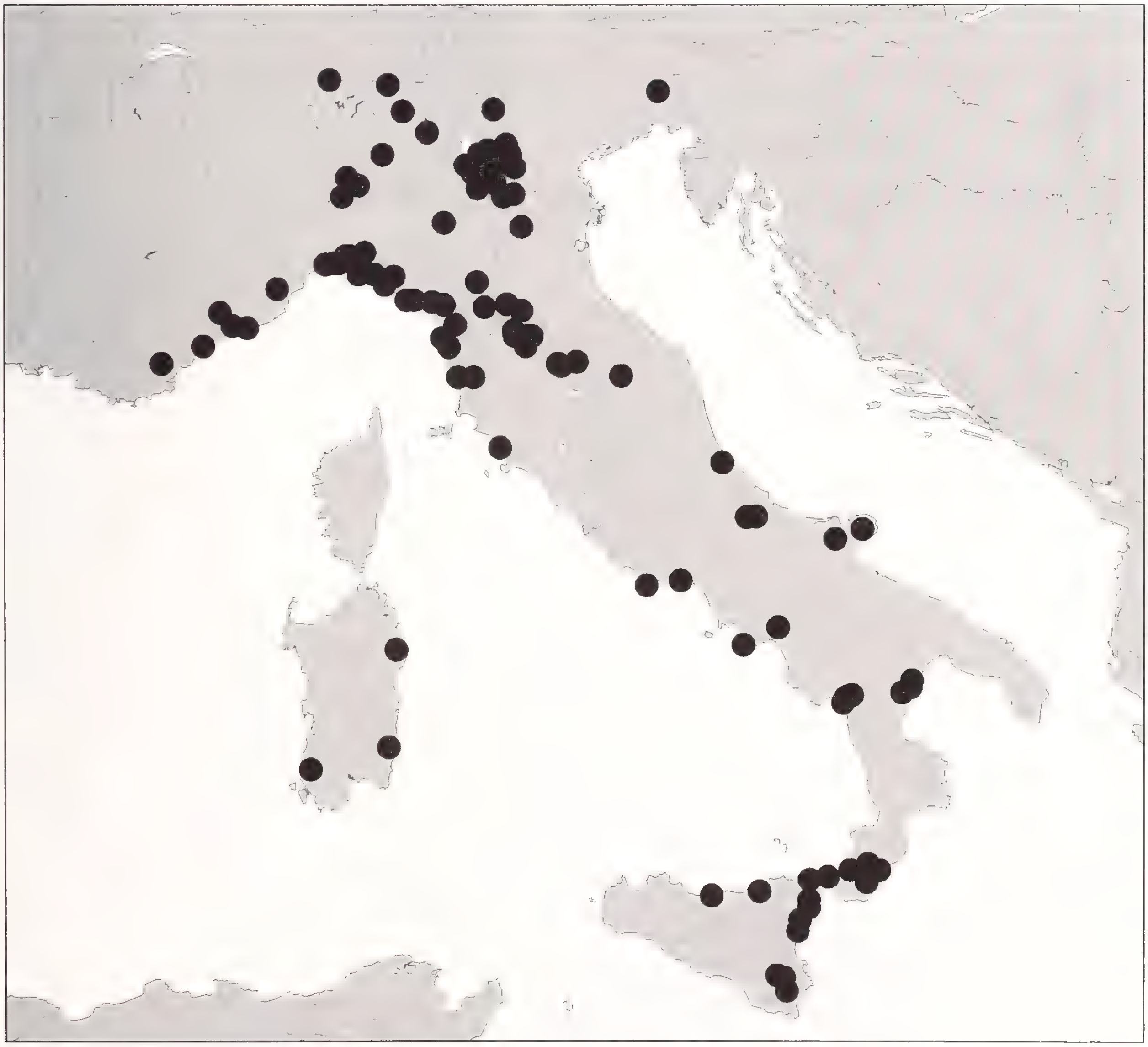
Diagnosis: In general appearance highly similar to *M. apicalis* (Fig. 1), distinguished as follows:

Coloration on average (!) slightly darker. Puncturation of head and pronotum on average slightly coarser and slightly more well defined.

♂: posterior margin of sternite VII in the middle with distinct convex projection (Figs. 2-3) (in *M. apicalis* weakly convex) and, especially in the middle, with darker, stouter, and longer modified setae; sternite VIII as in Fig. 4; aedeagus with ventral process of distinctive morphology: deeply bifid, apices widely separated, and subapically dentate (best visible in lateral aspect) (Figs. 5-7).

Intraspecific variation and comparative notes: Apart from the coloration, intraspecific variation is not pronounced. From all its congeners, *M. perniger* is readily distinguished by the distinctive morphology of the aedeagus, which is most similar to that of *M. maronitus* (Saulcy) from the Eastern Mediterranean and *M. bucharicus* Bernhauer from Middle Asia. For separation from the similar *M. apicalis*, whose distribution partly overlaps with that of *M. perniger* see diagnosis above.

Distribution and bionomics: *Medon perniger* is evidently an Adriato-Mediterranean element, whose distribution is confined to Italy, including Sicily and Sardinia, to southeastern France (Provence) and southern Switzerland (Map 3). It is here recorded from France and Switzerland for the first time. An occurrence in Turkmenistan (see material examined) would be far outside this range and the record should be considered doubtful until it is confirmed; quite possibly, the specimens were mislabelled. Apparently, the species is absent from Corsica and Elba, where *M. apicalis* has been collected frequently; however, both species have been found in the same locality on various occasions (see the distribution section below *M. apicalis*).



Map 3: Distribution of *Medon perniger* Coiffait in Italy and adjacent regions, based on revised records.

Unlike *M. apicalis*, most of the specimens listed above were not caught on the wing, but found in the leaf litter of various kinds of forests (oak, chestnut, etc.), under hay, or in nests of *Talpa* and *Apodemus*. OSELLA & ZANETTI (1974) frequently recorded the species (as *M. apicalis*) from mole nests, often in large numbers (up to 72 specimens per nest). Interestingly, they observed that *M. perniger* and *M. ripicola* appear to exclude each other in mole nests, with the former preferring drier situations and the latter occurring in damp habitats. The labels attached to the examined specimens indicate relatively low altitudes below 1000 m. With few exceptions, all the nest records examined are from the winter months. Flying specimens were collected in spring and summer (April through July, and September). On two occasions, the species was found at light sources (April, September). Three times in May and once in November it was collected from flood debris. Adult beetles were taken throughout the year, though only relatively few specimens were found in July and August.

3.3. *Medon sericellus* (Fairmaire, 1860)
(Figs. 8-12, Map 2)

Lithocharis sericella Fairmaire, 1860 (FAIRMAIRE 1860: 159f).

Type: Neotype ♂, here designated: Gde Kabylie: Yakouren, forêt Beni-Ghobri, 800m, – V.1953, G. Fagel / G. Fagel det., 1954: Medon apicalis Kr / Neotypus ♂ *Lithocharis sericellus* Fairmaire desig. V. Assing 2003 / Medon sericellus (Faimaire), det. V. Assing 2003 (IRSNB).

Comments: *Lithocharis sericellus* was described by FAIRMAIRE (1860) based on material from Bône, Algeria. Shortly after the description, the name was placed in the synonymy of *Medon apicalis*, where it has remained ever since (see e.g. FAUVEL 1886; BERNHAUER & SCHUBERT 1912). The type material was looked for, but not found, in the collections of the MNHNP (personally) and of the IRSNB by the curator in charge (D. DRUGMAND, Bruxelles, pers. comm. 2003). Thus, it must be regarded as lost. Due to the similarity of the Algerian species redescribed in this section and of *Medon apicalis*, as well as the fact the the sexual characters of *Medon* species were usually neither illustrated nor described in detail in the 19th century, the original description can be attributed either to *Medon apicalis* or to the material listed in this section. I have not seen any specimens of *M. apicalis* from Algeria (or Tunisia), so that the presence of this species in Algeria is doubtful. Consequently, the material from Grande Kabylie is here treated as conspecific with the type material of *M. sericellus* and, in the interest of the stability of nomenclature, a neotype is designated.

Additional material examined (total: 22 exs.):

Algeria: 13 exs., Grande Kabylie, Yakouren, forêt Beni-Ghobri, 800 m, V.1953, leg. Fagel (IRSNB, cAss); 3 exs., Grande Kabylie, forêt de Akfadou, Tala Kitan, 1100 m, 18.V.1953, leg. Fagel (IRSNB); 2 exs., Grande Kabylie, Forêt d´Akfadou, 9 km W Adekar, 1300 m, 17.V.1988, leg. Besuchet, Löbl & Burckhardt (MHNG, cAss); 2 exs., Grande Kabylie, Djebel Bou-Berak, 350 m, 19.V.1988, leg. Besuchet, Löbl & Burckhardt (MHNG); 1 ex., Atlas de Blida, Chréa, Les Glacières, 1100 m, 3.V.1988, leg. Besuchet, Löbl & Burckhardt (MHNG).

Tunisia: 1 ex., 25 km W Jendouba, ca. 10 km N Ghardimaou, Aïn Soltane, 36°29N, 08°19E, 670 m, litter of oak forest, 27.XII.2004, leg. Assing (cAss).

Diagnosis: In external characters indistinguishable from *M. apicalis* (Figs. 8-9); separated from that species only by the male primary and secondary sexual characters:

♂: posterior margin of sternite VII in the middle concave (Fig. 10); aedeagus of highly distinctive morphology, apically very long and acute, both in lateral and in ventral view (Figs. 11-12).

Comparative notes: From other species of the *M. apicalis* group, *M. sericellus* is reliably distinguished only by the shape and chaetotaxy of the male sternite VII and by the distinctive morphology of the aedeagus.

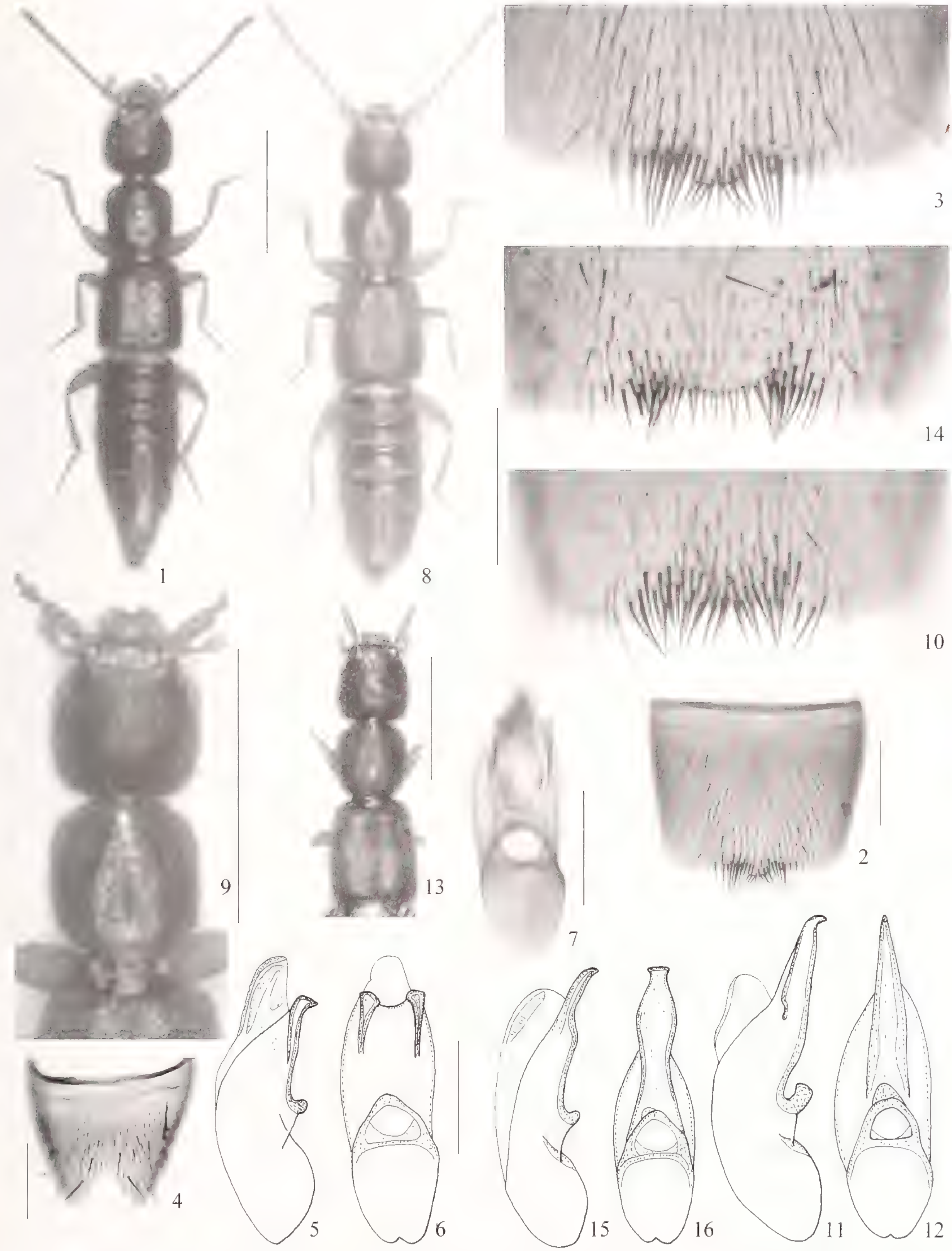
Distribution and bionomics: *Medon sericellus* has become known only from central northern Algeria and from northwestern Tunisia (Map 2), where the species was collected at altitudes of 350-1300 m in May and December.

3.4. *Medon oromii* sp. n. (Figs. 13-16)

Holotype ♂: Gran Canaria, 22-V-91, Bco. del Risco, P. Oromí / Holotypus ♂ *Medon oromii* sp. n. det. V. Assing 2003 (DZUL).

Diagnosis: 3.9 mm. Coloration: head dark brown; pronotum reddish brown; elytra and antennae rufotestaceous; abdomen reddish brown with the apex lighter; legs testaceous.

Head weakly oblong (Fig. 13); eyes slightly more than half the length of postocular region in dorsal view; puncturation relatively dense, but shallow, relatively fine, ill defined, and not very conspicuous in the pronounced microreticulation; dorsal surface matt.



Figs. 1-16. *Medon perniger Coiffait* (1-7), *M. sericellus* (Fairmaire) (8-12), and *M. oromii* sp. n. (13-16): Habitus (1, 8); forebody (9, 13); male sternite VII (2); posterior margin of male sternite VII (3, 10, 14); male sternite VIII (4); aedeagus in lateral and in ventral view (5-7, 11, 12, 15, 16). Scale bars: 1, 8, 9, 13: 1.0 mm; 2-7, 10-12, 14-16: 0.2 mm.

Pronotum slightly narrower than head and approximately as wide as long (Fig. 13); puncturation extremely fine, barely noticeable; surface matt due to pronounced microreticulation.

Elytra large and long, approximately 1.25 times as wide and at suture 1.15 times as long as pronotum (Fig. 13); puncturation dense and slightly granulose, much more distinct than that of pronotum; surface more shining than that of head and pronotum. Hind wings fully developed.

Abdomen with fine and dense puncturation; posterior margin of tergite VII with palisade fringe.

♂: protarsomeres I - IV not dilated; posterior margin of sternite VII of similar morphology and chaetotaxy as that of *M. apicalis* (Fig. 14) Aedeagus of highly distinctive morphology, with long, slender, and apically dilated ventral process (Figs. 15-16).

Etymology: The species is dedicated to Dr. Pedro Oromí, La Laguna, who collected the holotype and who has contributed so much to the current state of knowledge of Canarian Coleoptera.

Comparative notes and systematics: Among its Western Palaearctic congeners, *M. oromii* is readily identified especially by the extremely fine puncturation and pronounced microreticulation of the pronotum and by the distinctive morphology of the aedeagus. The morphology and chaetotaxy of the male sternite VII suggests that it belongs to the *M. apicalis* group. The aedeagus is most similar to that of *M. sericellus*.

The only West Palaearctic congeners with a similarly pronounced microsculpture on the pronotum are *M. feloi* from La Palma, *M. antricola* from El Hierro, the Canarian endemic *M. subcoriaceus*, and the Madeiran endemic *M. vicentensis*. All these species have strongly reduced eyes, except for *M. subcoriaceus*, which is distinguished from *M. oromii* by an oblong head, relatively dark coloration, and completely different male sexual characters.

Distribution and bionomics: The long wings and fully developed eyes would suggest that *M. oromii* is a widespread species, but currently it is known only from Gran Canaria, Canary Islands. Nothing is known about its natural history. Strangely, no further material of this species has become available, despite the fact that the staphylinid fauna of the Canaries is comparatively well studied.

3.5. *Medon dilutus* (Erichson, 1839)

In the Western Mediterranean, *Medon dilutus* is represented by three morphs, two of more or less uniformly rufous to ferrugineous coloration with shorter elytra and slightly smaller eyes and one usually with a coloration similar to that of *M. castaneus* (i.e. head, central part of pronotum, and abdominal segments blackish; elytra, pronotal margins, abdominal apex, and appendages lighter), with longer and broader elytra, and with slightly larger eyes. Based on slight differences in the shape of the aedeagal apex, the light-coloured short-winged morph can again be subdivided into fractions: one with an broader aedeagal apex with subparallel sides, distinct apico-lateral angles, and a small medio-apical emargination (Figs. 28-29), and one with curved sides, indistinct apico-lateral angles, and a large medio-apical emargination (Figs. 22-23), a condition also found in the long-winged morph. I have been unable to find other constant differences in the primary and secondary sexual characters. Since these morphs show a zoogeographically plausible allopatric distribution pattern, their previously proposed subspecific status is here maintained. As no material of *Lithocharis spelaea* Scriba, 1870 or its synonym *Medon dilutus breuili* Jeannel, 1921 was available for examination, their status still requires clarification. The types of both names were collected in caves in Valencia (Spain). JEANNEL & JARRIGE (1949) provide a very detailed illustration of a male of *M. dilutus breuili*, demonstrating that the eyes are considerably smaller than in *M. dilutus*. This and the fact that the type locality is within the distribution range of *M. dilutus cephalus* suggests that *M. spelaeus* (Scriba) represents a distinct species rather than a subspecies.

Remarkably, a comparison of the Western Mediterranean subspecies of *M. dilutus* with material of the widespread *M. pythonissa* (Saulcy, 1864) from the Eastern Mediterranean yielded no constant differences. In external appearance the latter is difficult to separate from *M. d. quadriceps*. It usually has an uniformly blackish pronotum, darker elytra, a somewhat coarser and sparser puncturation on the head and pronotum, slightly larger eyes, often an infuscated basal antennomere, but there are also transitions. The male secondary sexual characters are identical to those of the western subspecies, and the aedeagal apex is of similar morphology as that of *M. d. dilutus*. These observations suggest that *M. pythonissa* is conspecific with *M. dilutus* and that it should be regarded as a subspecies of this polytypical species, which apparently has a circum-Mediterranean distribution: *M. dilutus dilutus*, *M. d. cephalus*, and *M. d. quadriceps* in the northwest and southwest, respectively, of the Mediterranean basin and *M. d. pythonissa* representing the species in the eastern parts of the Mediterranean (Map 5).

3.5.1. *Medon dilutus dilutus* (Erichson, 1839)
(Figs. 24-29, Maps 4-5)

Lithocharis diluta Erichson, 1839 (ERICHSON 1839: 514).

Lithocharis oppidana Kraatz, 1857 (KRAATZ 1857: 711f) synonymy confirmed.

Medon dilutus meridionalis Bordoni, 1980 (BORDONI 1980: 98) **syn. n.**

Medon dilutus: GUSAROV 1992: 22f; invalid lectotype designation.

Types examined: *L. diluta*: Holotype ♀: 6364 / diluta Er. Berol. Er. / Lectotypus ♀ Lithocharis diluta Erichson V. Gusarov des. 1991 / Medon dilutus (Er.) ♀ Gusarov det. 1991 / Holotypus Lithocharis diluta Erichson labelled by Zool. Mus. Berlin, 7.2003 / Hist.-Coll. (Coleoptera) Nr. 6364 Lithocharis diluta Er., Berlin, Erichson, Zool. Mus. Berlin (MNHUB).

L. oppidana: Lectotype ♂ [remounted, aedeagus dissected], present designation: Berol. / Mayer / oppidana mihi / Syntypus / Coll. Kraatz / ♂ / Coll. DEI Eberswalde / Lectotypus ♂ *Lithocharis oppidana* Kraatz desig. V. Assing 2003 / Medon dilutus (Erichson) det. V. Assing 2003 (DEI). Paralectotype ♀: Berlin, Calix / oppidana Kr. * / Syntypus / Coll. Weise / Coll. DEI Eberswalde / Paralectotypus ♀ *Lithocharis oppidana* Kraatz desig. V. Assing 2003 / Medon dilutus (Erichson) det. V. Assing 2003 (DEI).

M. dilutus meridionalis: Holotype ♂: prov. di Bari, grotta di Cassano, 14.XI.1908, Dr. A. Andreini / HOLOTYPUS / Medon dilutus meridionali ssp. n. det. Bordoni 1980 / Medon dilutus meridionalis Bord. Gusarov det. 1991 / Medon dilutus (Erichson) det. V. Assing 2003 (cBor). Paratypes: 1♂ [teneral], 3♀♀: same data as holotype (cBor).

Comments: The original description of *Lithocharis diluta* is based on "ein einziges weibliches Exemplar" from the Erichson collection, which consequently has holotype status. Thus, the lectotype designation by GUSAROV (1992) is invalid. The holotype represents the light-coloured morph (similar to material from Sardinia and Spain).

According to KRAATZ (1857), there are several syntypes of *Lithocharis oppidana*, which were collected "unter feuchtem Laube von den Herren Mayer und Calix". Two of these syntypes were found in the Kraatz collection; they are conspecific with the holotype of *M. dilutus* (Erichson). In order to secure the present interpretation and the long-standing synonymy with *Medon dilutus*, the male syntype is here designated as the lectotype.

According to BORDONI (1980), *M. dilutus meridionalis* is characterized by large body size, light coloration, elongate appendages, less convex eyes, and the different shape of the apex of the aedeagus. Regarding both external characters and the shape of the aedeagus the types are indistinguishable from Central European *M. dilutus dilutus* (see Figs. 25-26, 28-29), so that the hypothesis that the population in southern Italy represents a distinct subspecies is not supported and *M. d. meridionalis* is considered a junior synonym of *M. d. dilutus*.

Additional material examined (total: 25 exs.):

Germany: Berlin/Brandenburg: 1 ex., Brieselang (DEI); 4 exs., Eberswalde ["Neustadt"] (DEI, NHMW); 1 ex., Berlin env. (DEI); 3 exs. [2 with worker of *Lasius fuliginosus* attached to the pin], Forst Dubrow, coll. Neresheimer (DEI). **Sachsen:** 1 ex., Rauden (DEI).

Austria: Niederösterreich/Wien: 6 exs., Wien, Lobau, mole nest, 21.III.1926, leg. Beier (NHMW, cAss). **Burgenland:** 2 exs., Zurndorf, leg. Franz (NHMW)

Czech Republic: 2 exs., Praha (NHMW); 1 ex., Brandys n. L. (NHMW).

Hungaria: 1 ex., NW Budapest, Mt. Pilis (NHMW).

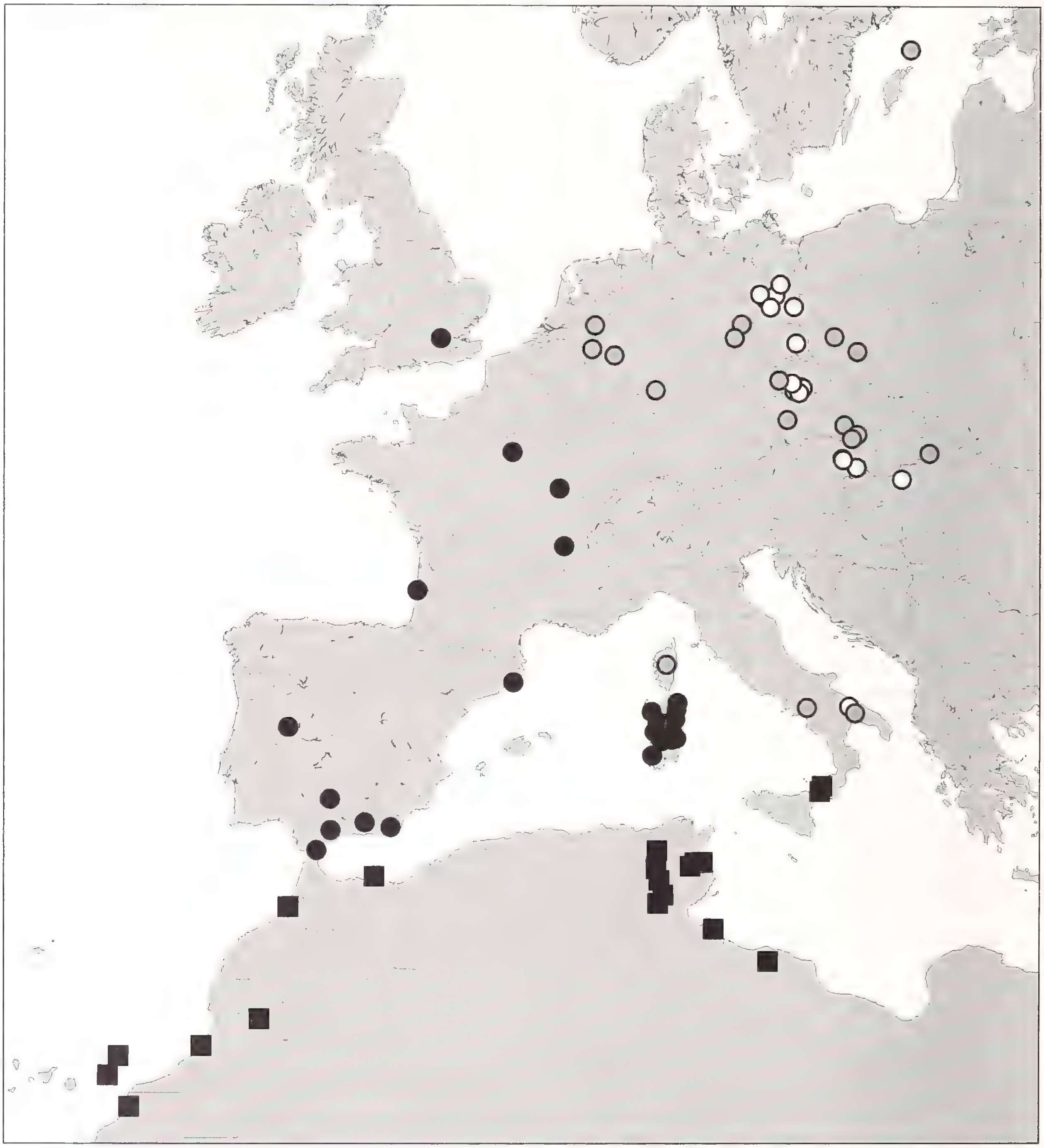
Locality not identified or not specified: 1 ex., without locality label, coll. Erichson (MNHUB); 2 exs. (DEI, NHMW).

Diagnosis: Since the nominal subspecies and *M. d. cephalus* are externally indistinguishable, the following description of characters, except for that of the aedeagus, refers to both taxa:

4.0-6.0 mm. Coloration more or less uniformly rufous to ferrugineous.

Head of very variable size and shape, weakly transverse to oblong (Figs. 17-21, 25-26), in small specimens sometimes not wider than pronotum (Fig. 18), in large specimens 1.2 times as wide as pronotum (Figs. 19, 26); eyes barely projecting from lateral outline of head, in dorsal view 0.35 - 0.45 times the length of postocular region; puncturation relatively fine, dense, well-defined, non-areolate, and usually more or less evenly distributed on whole dorsal surface (i. e. as dense in central dorsal area as in lateral areas), but density of puncturation rather variable (Figs. 17-21, 25-26); microsculpture absent or very shallow.

Pronotum usually with puncturation similar to that of head, with or without narrow unpunctured midline. Elytra 1.10 - 1.15 times as wide as pronotum, at suture approximately as long as, sometimes slightly longer than pronotum (Figs. 17-21, 25-26). Abdomen with very dense and fine puncturation; posterior margin of tergite VII with palisade fringe.



Map 4: Distributions of *Medon dilutus dilutus* (Erichson) (open circles; examined records), *M. d. cephalus* Koch (filled circles; examined records), and of *M. d. quadriceps* (Wollaston) (filled squares; examined records and literature records). Grey circles: literature records, referring to either *M. d. dilutus* and *M. d. cephalus*.

♂: protarsomeres I - IV distinctly dilated; sternite VII posteriorly moderately excavate, with two combs of palisade setae, margin between these combs straight and without conspicuous tufts of long dark setae (Fig. 24); sternite VIII with relatively small posterior excision; aedeagal apex with subparallel sides, pronounced apicolateral angles, and a small medio-apical emargination (ventral view) (Figs. 27-29).

♀: protarsomere I - IV not dilated.

Intraspecific variation: Both the nominal subspecies and *M. d. cephalus* are extremely variable. This particularly applies to the coloration, body size, the size and shape of the head, and the density of the puncturation (Figs. 17-21, 25-26). The head is usually relatively larger (e. g. in relation to the pronotum) and more transverse in larger than in smaller specimens (compare Figs. 18 and 19).

Comparative notes: Among Western Mediterranean *Medon* species, *M. dilutus dilutus* is readily identified by the dense, well defined, relatively fine, and usually more or less evenly spaced puncturation of head and pronotum, by the uniformly light coloration, and by the primary and secondary sexual characters. The somewhat similar *M. pocofer* has a flatter head, a more irregularly spaced puncturation of the head and pronotum, a relative wide impunctate midline of the pronotum, and shorter and broader pro-, meso-, and metatarsomeres. From *M. d. quadriceps* and *M. d. pythonissa* it is distinguished especially by the uniformly light coloration, the smaller eyes, and the shorter and narrower elytra, from *M. d. quadriceps* also by the different shape of the aedeagal apex.

Distribution and bionomics: *Medon dilutus dilutus* is apparently an Adriato-Mediterranean element (Maps 4-5), its distribution ranging from southern mainland Italy in the south at least to southern Central Europe (Poland, Austria, Germany, Hungary; material examined). The literature records from the western parts of Germany and from the Swedish island Gotska Sandön (LUNDBERG 1978) may refer to either this subspecies or to *M. d. cephalus*; the corresponding material was not available for examination. For additional literature records see also BOHÁČ (1985), HORION (1965), JANÁK (1993), KOCH (1968), KÖHLER & KLAUSNITZER (1998), KOLBE (1918), KORGE (1989), LUIGIONI (1929), and LUNDBERG (1995). The species is unknown from Belgium, Denmark, and the Baltic countries (BRUGE 2001; DRUGMAND 1989; HANSEN 1996; SILFVERBERG 1992). I know of only one recent record from Germany (KORGE 1989); from the Rhineland area, only two old records are known (KOCH 1968 1974), but they may refer to *M. d. cephalus*. In Italy, it is known from three localities in Campania and Puglia in the south of the mainland (BORDONI 1980; LUIGIONI 1929; SCHEERPELTZ 1958). It has also been recorded from Corsica (LUIGIONI 1929; SAINTE-CLAIRE DEVILLE 1906), but this record, too, probably refers to *M. d. cephalus*. The record of *M. dilutus* from the Crimea by GUSAROV (1989) was later corrected into *M. mersinus* Bordoni by GUSAROV (1992); *M. mersinus* is now a synonym of *M. d. pythonissa* (see ASSING 2004a).

On the whole, *M. dilutus dilutus* has been collected very rarely. On several occasions, the subspecies was found at the bases or under bark of old or dead oak trees, under bark of pine trees, in nests of various mammals (mole, mouse/vole, fox), in a nest of the ant *Lasius fuliginosus*, and in caves (material examined, and BOHÁČ (1985); BORDONI (1980); FRANZ (1938); HORION (1965); KORGE (1989); STROUHAL & BEIER (1928)). On one occasion, STROUHAL & BEIER (1928) found as many as 10 specimens in one apparently abandoned mole nest in Wien-Lobau, but no further specimens were recorded from a total of 188 nests examined. All these data suggest that the reproduction habitat is somewhat cryptic, subterranean, but essentially unknown. Flying specimens were recorded in May and June (HORION 1965). Adult beetles have been found almost throughout the year, but most records are from spring and autumn.

3.5.2. *Medon dilutus cephalus* Koch, 1938

(Figs. 17-23, Maps 4-5)

Medon dilutus cephalus Koch, 1938 (KOCH 1938: 140f)

Medon dilutus boeticus Jeannel & Jarrige, 1949 (JEANNEL & JARRIGE 1949: 361) **syn. n.**

Types examined: *M. dilutus cephalus*: Holotype ♂: LULA, Sard., 7.III.1912, A. Dodero / Medon dilutus / spec. nov. det. C. Koch / Type / Mikr. Pr. 104 / M. dilutus var. cephalus Koch det. C. Koch / Medon dilutus (Erichson) det. V. Assing 2003 (NHMB).

M. dilutus boeticus: Syntype ♀: Cueva de la D. Trinidad / Biospeologica 932 III 18 / Jeanneli m. det. Dr. Rambousek / Muséum Paris Ex Collection J. JARRIGE1976 / COTYPE / d. baeticus [sic] Jean. & Jar. / Medon dilutus (Erichson) det. V. Assing 2003 (MNHNP).

Comments: The holotype of *M. dilutus cephalus* was dissected prior to the present study. The aedeagus and apical abdominal segments are missing; as can be inferred from one of the labels attached to the specimen, they were mounted separately for microscopic examination probably by Koch himself.

The type of *M. dilutus boeticus* represents a – probably submacropterous – uniformly ferrugineous specimen with relatively short elytra. In all respects it is within the range of intrasubspecific variation of *M. dilutus cephalus*, hence the synonymy indicated above.

Additional material examined (total: 48 exs.):

Spain: Cataluña: 1 ex., Malgrat de Mar, 3.V.1959, leg. Liebmann (NHMW). **Estremadura:** 1 ex., Cáceres, Gata, 3.V.1957, leg.González (MHNG). **Andalucía:** 5 exs., Sierra de Alhamilla (AL), 1000 m, N-slope, 20.III.1994, leg. Assing, Wunderle (cAss, cWun); 2 exs., Sierra Nevada, Rio Genil, 37°08´26N, 03°24´01W, 1000 m, 24.II.2000, leg. Lompe (cAss); 1 ex., Sierra de Cordoba, leg. Franz (NHMW); 1 ex., San Roque (CA), leg. Comellini (MHNG).

France: 2 exs., Lyon env. (DEI); 1 ex., Fontainebleau, 23.V.1900 (MHNG); 1 ex., La Bonde, 10.XII.1903, leg. Fagniez (MHNG); 2 exs., Gironde, Biscarosse Plage, 25.-28.VII.1980, leg. Kiener (MHNG). **Corsica:** 1 ex., locality not specified (NHMW).

England: 1 ex., London, Richmond, 19.X.1998, leg. Owen (cOwe).

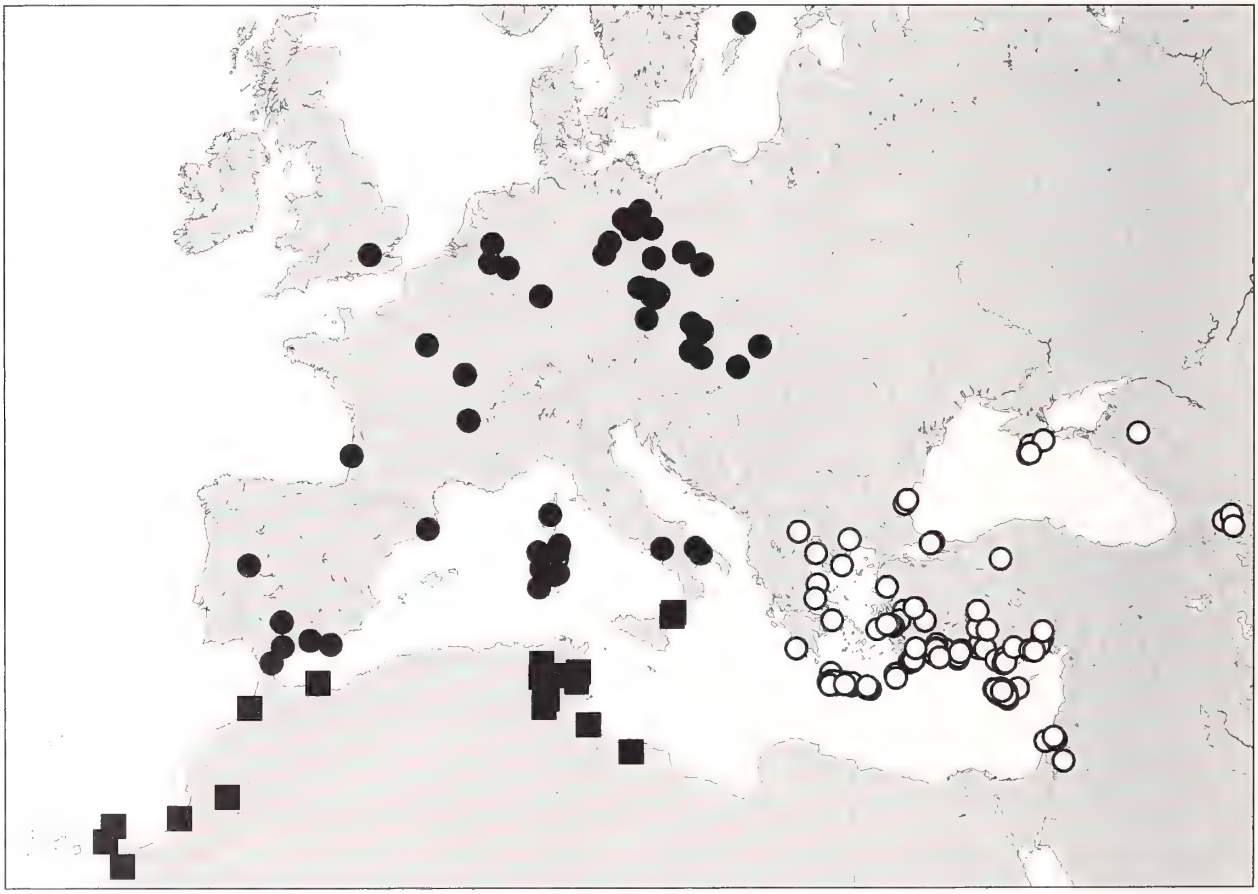
Italy: Sardegna: 1 ex., Mte. Chiesa (NHMB); 2 exs., Aritzo (NHMW); 1 ex., Aritzo, Mte. Genargentu, leg. Krüger (DEI); 2 exs., Golfo Aranci, III.1907, leg. Dodero (DEI); 1 ex., Seneghe, 2.V.1891, leg. Dodero (DEI); 1 ex., Seui (NHMB); 1 ex., Seui, 7.V.1902, leg. Dodero (NHMW); 2 exs., Seui, leg. Dodero (NHMW, cAss); 1 ex., N Bolotana (SS), 850 m, 13.IV.1992, leg. Scheuern (cAss); 1 ex., Onani (NU), 450m, 24.XI.1992, leg. Meloni (cZan); 1 ex., Lanusei (NU), 12.V.1980, leg. Torchia (UCBA); 1 ex., Padru (SS), XII.1999, leg. Fancello (cZan); 1 ex., Iglesias (CA), 8.III.2001, leg. Fancello (cZan); 1 ex., Sorgono, leg. Krausse (DEI); 1 ex., Campeda, 28.IV.1908, leg. Dodero (cAss); 1 ex., NE Sadali (NU), 850 m, 20.IV.1992, leg. Schawaller (SMNS).

Diagnosis: For a description of external and secondary sexual characters see the diagnosis of *M. d. dilutus* above.

♂: aedeagal apex in ventral view with curved sides, indistinct apico-lateral angles, and a large medio-apical incision (Figs. 22-23).

Intraspecific variation: Similar to that of *M. d. dilutus*.

Comparative notes: For separation from other Western Mediterranean species of *Medon*, see the comparative notes below *M. d. dilutus*. From *M. d. quadriceps* and *M. d. pythonissa* it is distinguished by the uniformly light coloration, the smaller eyes, and the shorter and narrower elytra, from *M. d. pythonissa* also by the different shape of the aedeagal apex.



Map 5: Distributions of *Medon dilutus dilutus* (Erichson) + *M. d. cephalus* Koch (filled circles), *M. d. quadriceps* (Wollaston) (filled squares), and *M. d. pythonissa* (Saulcy) (open circles), mainly based on examined records.

Distribution and bionomics: *Medon dilutus cephalus* is an Atlanto-Mediterranean element (Maps 4-5), its distribution ranging from southern Spain and Sardinia in the southwest and south to southern England in the north, possibly even to the Swedish island Gotska Sandön (see notes on the distribution of the nominal subspecies). In Sardinia it is apparently relatively common (see material examined). The records of *M. dilutus* from Corsica (LUIGIONI 1929; SAINTE-CLAIRE DEVILLE 1906) probably refer to this subspecies, but I have seen only a female from this island. In the British Isles, it is known from only three localities in southern England (ALLEN 1996; OWEN 1998, 2000). This subspecies has been found in similar habitats and under similar circumstances as *M. d. dilutus*. Several specimens were sifted from the leaf litter in a mixed stand of *Quercus ilex* and *Pinus* sp. in southern Spain (material examined).

3.5.3. *Medon dilutus quadriceps* (Wollaston, 1864)
(Figs. 30-32, Maps 4-5)

Lithocharis quadriceps Wollaston, 1864 (WOLLASTON 1864: 586).

Medon vitalei Bernhauer, 1936 (BERNHAUER 1936: 306f) **syn. n.**

Medon dilutus eremicus Koch, 1939 (KOCH 1939: 243f) **syn. n.**

Medon algiricus Jeannel & Jarrige, 1949 (JEANNEL & JARRIGE 1949: 361f).

Medon marocanum Coiffait, 1970a (COIFFAIT 1970a: 707) **syn. n.**

Medon mateui Coiffait, 1973b (COIFFAIT 1973b: 282) **syn. n.**

Types examined: *M. vitalei*: Holotype ♀: Castanea, 27.X.34, F. Vitale / Vitalei Brnh. Typus unic. Medon / Medon dilutus (Erichson) det. V. Assing 2003 (FMNH).

M. dilutus eremicus: Holotype ♀: Tauorga nordöstl. Trip., IV.38. G. Frey / Medon eremicus Koch det. C. Koch / Medon dilutus (Erichson) det. V. Assing 2003 (NHMB).

M. marocanus: Holotype ♂: IXMOART, B. SICAR. (MARR.), COBOS SANCHEZ / MUSEUM PARIS COLL H. COIFFAIT / HOLOTYPE / Medon marocanum Coiff. H. COIFFAIT det. 1969 / Medon dilutus (Erichson) det. V. Assing 2003 (MNHNP).

M. mateui: Holotype ♂: MAROC, env. Ifni, H. COIFFAIT / MUSEUM PARIS COLL H. COIFFAIT / HOLOTYPE / Medon mateui H. COIFFAIT det. 1973 / Medon dilutus (Erichson) det. V. Assing 2003 (MNHNP).

Comments: The original description of *Lithocharis quadriceps*, which is based on material from Lanzarote and Fuerteventura, leaves no doubt that the types are conspecific with the male non-type specimen seen from Fuerteventura. The original description of *M. vitalei* is explicitly based on a single female. The holotype was examined and found to be a small specimen of the morph here referred to as *M. dilutus quadriceps*, hence the synonymy indicated above. Similarly, no evidence was found suggesting that the examined holotypes of *M. dilutus eremicus* and *M. marocanus* should represent a distinct (sub-) species, so that both names are placed in the synonymy of *M. d. quadriceps*.

COIFFAIT (1973b) compares *M. mateui* with *M. marocanus* stating that the former is distinguished from the latter by the dilated male protarsi, the more shallowly convex posterior margin of the male sternite VII, and the apex of the aedeagus having the shape of a semicircle and lacking the median incision. An examination of the holotype of *M. mateui*, however, revealed no such differences in the degree of dilatation of the male protarsi or in the shape of the male sternite VII. Moreover, the apex of the aedeagus clearly has a median incision, though this incision is somewhat smaller than is usually the case in *M. dilutus*. However, this teratological malformation is a common phenomenon in the genus and is present also, for instance, in the holotype of *M. aquitanicus* Coiffait. Aside from the somewhat lower body size and the much smaller head, the holotype of *M. mateui* is, in fact, strikingly similar to the holotype of *M. marocanus*. Since there is no evidence that it represents a distinct species, *M. mateui* is here synonymized with the senior name *M. dilutus quadriceps*.

Additional material examined (total: 23 exs.):

Tunisia: 1 ex., Kasserine (=Al Qasrayn), II.1941, leg. Demoflys (cTro); 3 exs., Zarzis (=Jarjis), II.1951, leg. Demoflys (cTro, cAss); 1 ex., Zarzis, VI.1944, leg. Demoflys (cTro); 1 ex., Gafsa (MHNG); 1 ex., Qibili ["Kebili", 33°41N, 08°58E] (MHNG); 1 ex., Tālah ["Thala", 35°34N, 08°40E] (cAss); 1 ex., ca. 40 km W Sousse, 35°54N, 10°15E, roadside, under stones, 30.XII.2004, leg. Assing (cAss).

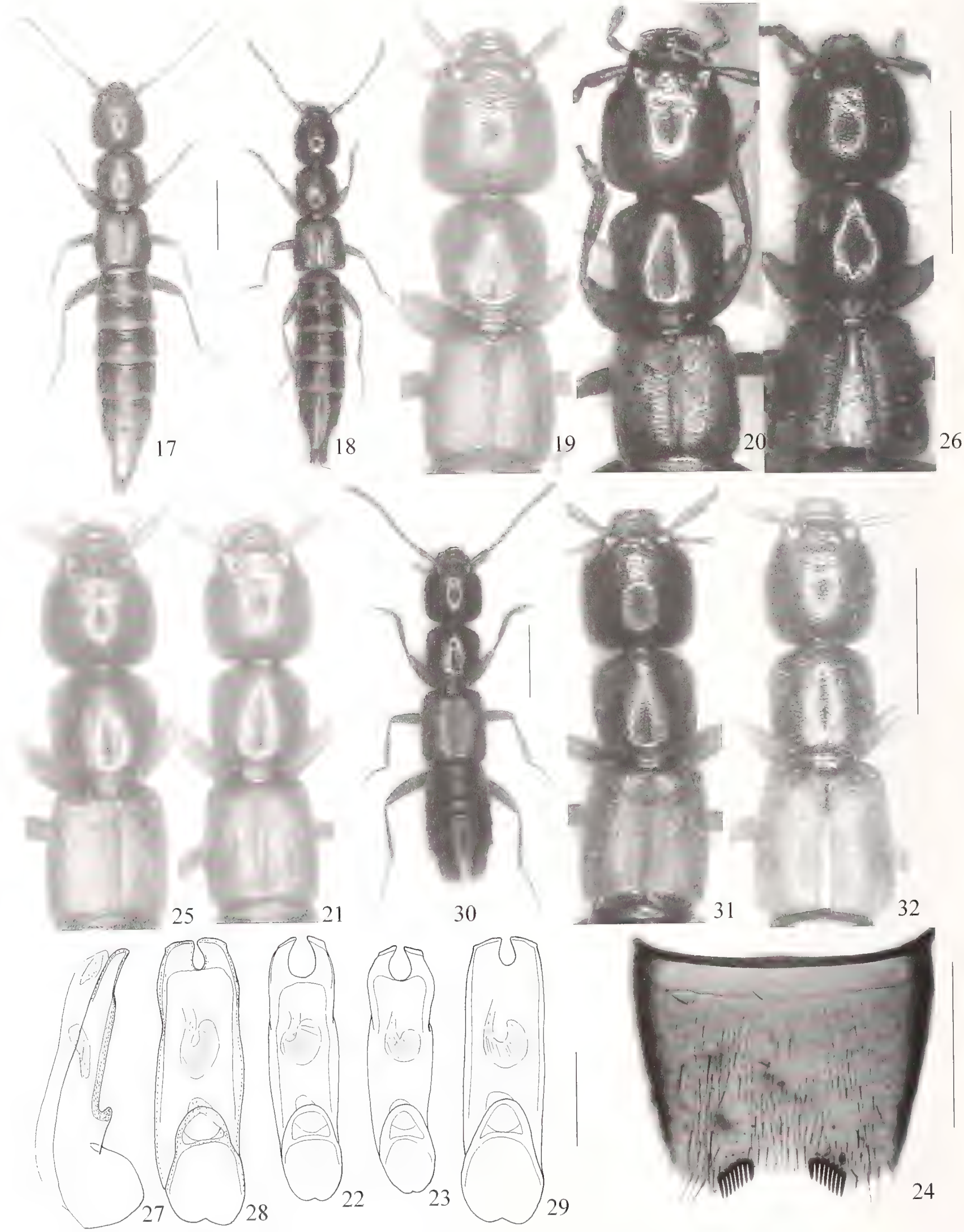
Morocco: 1 ex., Oued Sebou, IV.1961, leg. Comellini (cAss); 1 ex., Anti-Atlas, Agard-Oudad (?), 1200m, 7.-8.IX.1990, leg. Annot (DEI).

West Sahara: 1 ex., Meseied near Al Aaiun, leg. Franz (NHMW).

Portugal: Azores: 4 exs. [identification uncertain], Sao Miguel, leg. Franz (NHMW, cAss).

Canary Islands: 1 ex., Fuerteventura, Cueva del Llano, 4.IV.1992, leg. Oromí (cAss).

Italy: Sicilia: 1 ex., locality not specified, leg. Vitale (UCBA); 1 ex., Messina, leg. Vitale (cAss).



Figs. 17-32. *Medon dilutus dilutus* (Erichson) (24-29), *M. dilutus cephalus* Koch (17-23), and *M. dilutus quadriceps* (Wollaston) (30-32): Habitus (17: Sardinia; 18: Andalucia; 30: Tunisia); forebody (19: Sardinia, 20: holotype of *M. dilutus cephalus* Koch; 21: Andalucia; 25: Wien; 26: holotype of *M. dilutus meridionalis* Bordoni; 31: Tunisia: 32: Fuerteventura); male sternite VII (24: Prague); aedeagus in lateral and in ventral view (27, 28: Wien; 29: Prague; 22: Andalucia; 23: Sardinia;). Scale bars: 17-21, 25-26, 30-32: 1.0 mm; 24: 0.5 mm; 22-23, 27-29: 0.2 mm.

Diagnosis: This subspecies is distinguished from the nominal subspecies and from *M. d. cephalus* as follows:

Coloration highly variable, but usually similar to that of *M. castaneus* and *M. subcoriaceus*: Head, central part of pronotum, and abdominal segments III to anterior half of VII usually dark brown to blackish brown; margins of pronotum near anterior angles broadly, in other places narrowly ferrugineous; elytra and abdominal apex testaceous, rufous, or brown; legs and antennae more or less rufous.

Elytra larger, approximately 1.3 times as wide and at suture 1.1 times as long as pronotum. Eyes of somewhat variable size, but on average larger, approximately half as long as temples in dorsal view (Figs. 30-32).

♂: aedeagal apex as in *M. d. cephalus* (cf. Figs. 22-23).

Intraspecific variation: The extent of intrasubspecific variation is similar to that observed in the other subspecies, especially as regards coloration, body size, as well as size and shape of the head. One nanistic specimen seen from Morocco represented a transitional state between the nominal subspecies and *M. d. quadriceps* in that it had a light coloration and relatively long, but rather narrow elytra. The specimens from the Azores have a very pronounced microsculpture on the head and pronotum; the latter is of uniformly dark coloration. Unfortunately, only females were available from the Azores, so that their present interpretation must be considered tentative.

Comparative notes: *Medon d. quadriceps* is highly similar to the Ponto-Mediterranean *M. d. pythonissa*, but distinguished by on average finer puncturation of the head and pronotum, the lower average size of the eyes, the lighter margins of the pronotum, the darker elytra, and the different shape of the aedeagus apex (in *M. d. quadriceps* similar to that of *M. d. cephalus* and in *M. d. pythonissa* similar to that of the nominal subspecies).

Distribution and bionomics: The distribution of *M. d. quadriceps* (Maps 4-5) includes Northwest Africa from Tunisia to southern Morocco and West Sahara, the Canary Islands (Fuerteventura, Lanzarote), and Sicily, possibly also the Azores (material examined; see also HORION (1965), MACHADO & OROMÍ (2000), and NORMAND (1935)). Horion (1965) reports it from the Hoggar range in southern Algeria. Material of this subspecies has been collected in various habitats such as caves or a sparrow´s nest (NORMAN 1935), but its real reproduction habitat must be considered unknown. The distribution suggests that it is adapted especially to hot and dry regions. The material examined was collected in February, April, June, October, and December.

3.6. *Medon subcoriaceus* (Wollaston, 1864)
(Figs. 33-37)

Lithocharis subcoriaceus Wollaston, 1864 (WOLLASTON 1864: 586).

Material examined (total: 1097 exs.; see also material listed in ASSING (1999a, 2000) and ASSING & WUNDERLE (1999)):

Canary Islands: Tenerife: 4 exs., Pico del Ingles, 960 m, 4.&13.IV.1992, leg. Assing (cAss); 1 ex., same locality, 950 m, 28.XI.1996, leg. Schülke & Grünberg (cSch); 2 exs., La Laguna, 750 m, 4.IV.1992, leg. Assing (cAss); 16 exs., El Bailadero, 900 m, 3.IV.1992, leg. Assing (cAss); 22 exs., Anaga, Chamorga, 700 m, 5.IV.1992, leg. Assing (cAss); 1 ex., Anaga, Chinobre, 850 m, 5.IV.1992, leg. Assing (cAss); 1 ex., Anaga, E Chinobre, Bco. d. Corral Viejo, 600 m, 5.XII.1996, leg. Schülke (cSch); 2 exs., E Chinobre, 700 - 800 m, 24.XI.1996, leg. Schülke & Grünberg (cSch); 2 exs., NE Chinobre, 850 m, 8.VII.1995, leg. Zerche (DEI); 1 ex., Anaga, Taborno, 1020 m, 5.IV.1992, leg. Assing (cAss); 14 exs., Anaga, leg. Franz (NHMW); 4 exs., Montes de las Mercedes, leg. Franz (NHMW); 1 ex., Las Mercedes, 750 m, 4.IV.1992, leg. Zerche (DEI); 1 ex., Anaga, Estanque, 28°34N, 16°10W, 26.III.2000, leg. Lompe (cAss); 1 ex., Anaga, 28°34N, 16°10W, 25.III.2000, leg. Lompe (cAss); 2 exs., Anaga, Atalaya del Sabinal, 1.5 km SE Lomo de la Bodegas, 500 - 550 m, 11.I.2002, leg. Schülke (cSch); 1 ex., Anaga, 1 km S Lomo de las Bodegas, road to Chamorga, 650 m, 11.I.2002, leg. Schülke (cSch); 16 exs., Anaga, 3 km E El Bailodero, 900 m, 3.IV.1992, leg. Zerche (DEI); 17 exs., El Bailodero, 800 m, 2.VII.1995, leg. Zerche (DEI); 1 ex., Anaga, Cabezo del Tejo, 730 m, 5.VII.1995, leg. Zerche (DEI); 13 exs., Anaga El Pijaral, 800-850 m, laurisilva, 4.VII.1995, leg. Zerche (DEI); 7 exs., Anaga, Vueltas de Taganana, 780-850 m, *Erica* forest, 5.VII.1995, leg. Zerche (DEI); 2 exs., same data, but 450 m, laurisilva (DEI); 9 exs., Anaga, Cruz del Carmen, 900 m, *Erica* litter, 2.VII.1995, leg. Zerche (DEI); 5 exs., Bosque de la Esperanza, W Las Rosas, 1000 m, 26.11.1996, leg. Schülke & Grünberg (cSch); 1 ex., Esperanza, 1200 m, 6.VII.1995, leg. Zerche (DEI); 1 ex., Orotava valley, Aguamansa, 1080 m, 25.XII.1995, leg. Stüben & Bahr (DEI); 9 exs., Teno, Erjos, 900 m, 8.-10.IV.1992, leg. Assing (cAss); 3 exs., Erjos, 12.III.1996, leg. Meybohm (cAss); 1 ex., Teno, N Erjos, 700 m, 30.XI.1996, leg. Schülke & Grünberg (cSch); 2 exs., Teno, Monte del Agua, 900-950m, 1.&10.VII.1995, leg. Zerche (DEI); 1 ex., Bajamar, 27.IX.1965, leg. Benick (cAss); 2 exs., Bco. del Infierno, 500 m, 9.IV.1992, leg. Assing (cAss); 3 exs., Vueltas de Taganana, VI.1957, leg. Fernández (NHMW); 4 exs., locality not specified (NHMW). **Gran Canaria:** 98 exs., NNW Lanzarote, Bco. de la Virgen, 500 m, degraded laurisilva, 20.XII.1997, leg. Assing (cAss); 7 exs., E Osorio, SW El Palmar, 600m, degraded laurisilva, 20.XII.1997, leg. Assing (cAss); 10 exs., Pinar de Tamadaba, 1200 m, pine forest, 22.XII.1997, leg. Assing (cAss); 3 exs., Pinar de Tamadaba, 1275m, 28°03N, 15°41W, pine forest with *Erica arborea*, 4.II.1998, leg. Zerche (DEI); 1 ex., S Moya, Los Tilos, 400 m, laurisilva, 23.XII.1997, leg. Assing (cAss); 9 exs., W Moya, El Palmital, 500 m, 23.XII.1997, leg. Assing (cAss); 2 exs., Cruz de Tejeda, 1600 m, 25.XII.1997, leg. Assing (cAss); 1 ex., Tejeda, leg. Gaudin (cSch); 10 exs., Valleseco, leg. Franz (NHMW); 9 exs., laurisilva near Moya, leg. Franz (NHMW); 1 ex., Isleta near Las Palmas, leg. Franz (NHMW); 1 ex., Bco. de Mogán, 27°54N, 15°42W, 355 m, *Euphorbia obtusifolia* + *Echium decaisnei*, sifted, 7.II.1998, leg. Zerche (DEI). **La Palma:** 1 ex., Los Tilos, leg. Franz (NHMW). **El Hierro:** 1 ex., Los Gramales, 21.IV.1985, leg. Oromí (cAss); 9 exs., Valverde, leg. Franz (NHMW); 7 exs., El Golfo, leg. Franz (NHMW); 4 exs., El Golfo, S El Moncenal, 900 m, Fayal-Brezal, 9.XII.1996, leg. Schülke (cSch); 1 ex., Mirador de la Peña, 650 m, 10.-13.XII.1996, leg. Schülke & Grünberg (cSch); 2 exs., Sabina, leg. Franz (NHMW); 12 exs. [partly teneral], El Brezal near Tabano, 850/1205 m, fayal-brezal, 27°44N, 18°01W, 17.I.1998, leg. Behne (DEI); 1 ex., below Sabinosa, 95 m, 27°45N, 18°06W, *Eonium* sifted, 27.I.1998, leg. Behne (DEI); 31 exs., Lomo Blanco, 6 km W Frontera, 27°45N, 18°03W, 550 m, fayal-brezal, 25.I.1998, leg. Behne (DEI); 5 exs., El Gretime, 8 km W Frontera, 27°44N, 188°04W, 800 m, fayal-brezal, 21.I.1998, leg. Behne (DEI); 4 exs. [1 teneral], Mtn. Colorada, 10 km SW Frontera, 27°44N, 18°02W, 1050 m, 21.I.1998, leg. Behne (DEI); 1 ex., Camino de San Salvador near Tabano, 27°44N, 18°01W, 1325 m, fayal-brezal, 17.I.1998, leg. Behne (DEI). **La Gomera:** 1 ex., El Cedro, 1000 m, 27.X.1990, leg. Wunderle (cAss); 2 exs., El Cedro, 900 m, 2.XI.1990, leg. Wunderle (cAss, cSch); 35 exs., El Cedro, leg. Franz (NHMW); 2 exs., El Cedro, 29.VI.2002, leg. Klemm & Wisser (cSch); 4 exs., El Cedro, 1 km S Ermitá, 14.I.2002, leg. Schülke (cSch); 20 exs., El Cedro, Ermitá, 900 m, 17.&19.VII.1995, leg. Zerche (DEI); 4 exs. [1 teneral], El Cedro, 600 m, 2.I.1998, leg. Stüben & Bahr (DEI); 1 ex., S Las Creces, 21.II.-8.III.2001, leg. Arndt (cSch); 1 ex., N Laguna Grande, laurisilva, 14.I.2002, leg. Schülke (cSch); 2 exs., Camino Forestal La Meseta, 650 m, laurisilva, 15.VII.1995, leg. Zerche (DEI); 2 ex., barranco above Hermigua, laurisilva, 550 - 580 m, 16.&19.VII.1995, leg. Zerche (DEI); 6 exs., Bco. N La Laguna Grande, 1010-1050 m, laurisilva, 15.&17.VII.1995, leg. Zerche (DEI); 2 exs.; Raso de la Bruma, 1000 m, laurisilva, 18.VII.1995, leg. Zerche (DEI); 1 ex., Mirador de Alojera, 26.V.2003, leg. Contreras & Oromí (cOro); 2 exs., Cabecera del Bco. de Juel, 8.VIII.2002, leg. Oromí (cOro). **Fuerteventura:** 1 ex., Mte. de Betancuria, leg. Franz (NHMW).

Diagnosis: 4.0-5.2 mm. Habitus as in Fig. 33. Head brown to blackish; pronotum usually slightly lighter than head, more rarely of similar coloration; elytra light brown to brown; abdomen, except for the lighter apex, of similar coloration as head or pronotum; legs and antennae rufous to yellowish brown.

Head distinctly oblong, about 1.10 - 1.15 times as long as wide; eyes relatively large, in dorsal view usually slightly more than half the length of temples; puncturation very fine, dense, and more or less well-defined; microsculpture usually distinct, more rarely shallow, but always visible especially in lateral areas (Fig. 34).

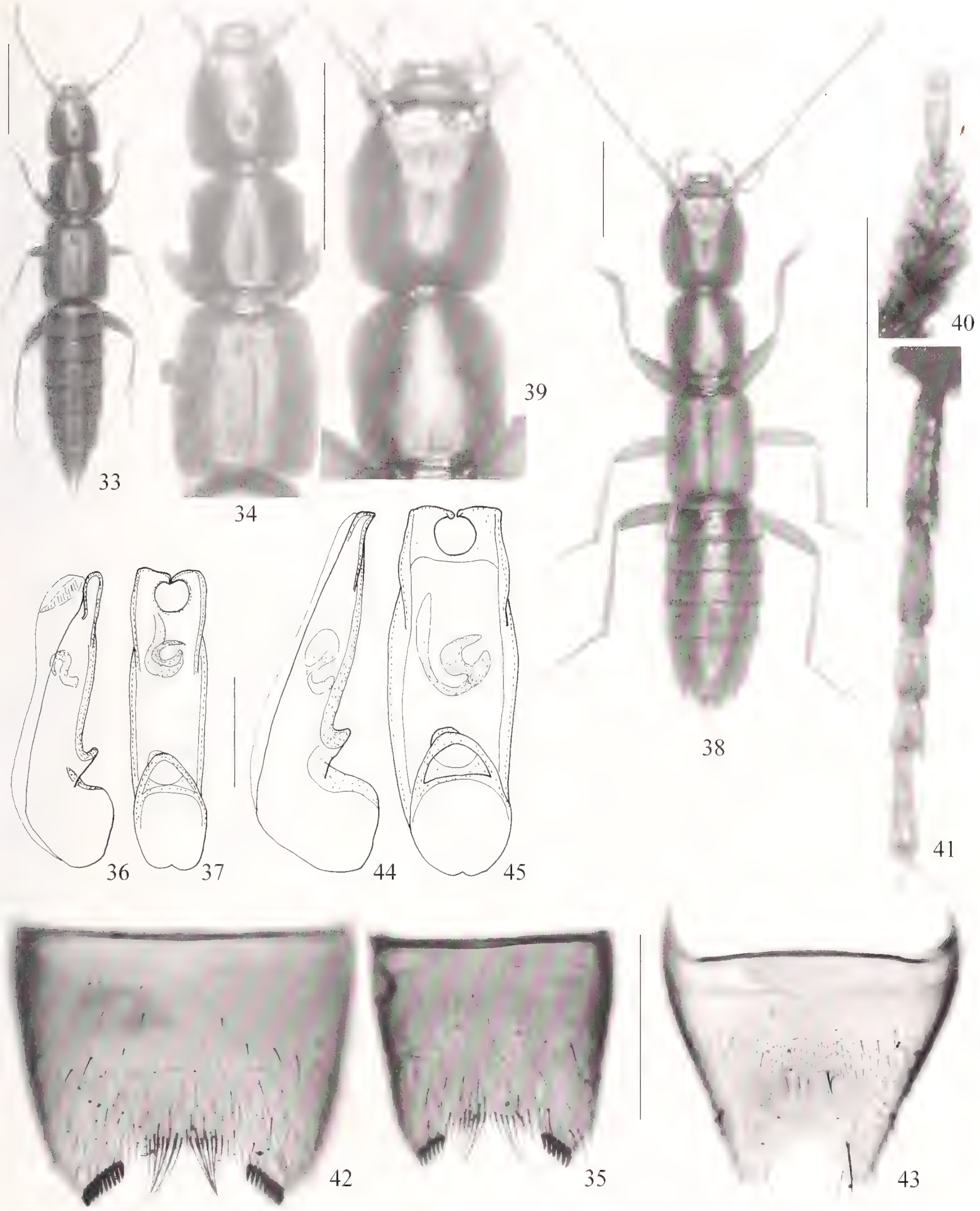
Pronotum 1.05 - 1.10 times as wide as head and approximately as wide as long; puncturation even finer than that of head, often barely noticeable in the pronounced microsculpture (Fig. 34).

Elytra relatively large, 1.2 - 1.3 as wide and at suture 1.10 - 1.15 times as long as pronotum (Fig. 34); punctuation dense, fine, and weakly granulose. Hind wings fully developed.

Abdomen narrower than elytra (Fig. 33); puncturation very dense and fine; posterior margin of tergite VII with palisade fringe.

♂: posterior margin of sternite VII deeply concave, with two combs of 5 - 8 palisade setae and on either side of middle with a tuft of long dark setae (Fig. 35); sternite VIII not distinctive; aedeagus of similar general morphology as that of *M. dilutus*, but apical part of different shape (Figs. 36 - 37).

Comparative notes: *Medon subcoriaceus* is readily identified by external characters alone, especially by its oblong head with a dense, fine, and well-defined puncturation and usually distinct microsculpture, by the extremely finely punctured and distinctly microsculptured pronotum, and the long elytra. In addition it is identified by the presence of tufts of long black setae at the posterior margin of the male sternite VIII (one on either side of middle) – a character otherwise exclusive to the following species, to *M. kabylicus*, and to the species of the *M. fusculus* group – as well as by the distinctive shape of the apex of the aedeagus.



Figs. 33-45. *Medon subcoriaceus* (Wollaston) (33-37) and *M. antricola* sp. n. (38-45): Habitus (33, 38); forebody (34); male sternite VII (35, 42); aedeagus in lateral and in ventral view (36, 37, 44, 45); head and pronotum (39); male protarsus (40); metatarsus (41); male sternite VIII (43). Scale bars: 33, 34, 38, 39: 1.0 mm; 35, 40-43: 0.5 mm; 36, 37, 44, 45: 0.2 mm.

Distribution and bionomics: *Medon subcoriaceus* is endemic to the Canary Islands. It occurs in all larger islands except Lanzarote (material examined; MACHADO & OROMÍ 2000) and is common everywhere except Fuerteventura, from where it is here recorded for the first time. The species was found in large numbers especially in the laurisilva, fayal-brezal, and other semi-natural woodland habitats of Tenerife, Gran Canaria, La Gomera, La Palma, and El Hierro, but also in semi-arid biotopes. The examined material was collected throughout the year; teneral adults were repeatedly observed in January.

3.7. *Medon antricola* sp. n. (Figs. 38-45)

Holotype ♂: El Hierro, JN-C/CO-3920, Cueva de Jinama, 26-IX-00, GIET leg. / Holotypus ♂ Medon antricola sp. n. det. V. Assing 2003 (DZUL). Paratypes: 1♂: El Hierro, JN-C/CO-3779, Cueva de Jinama, 26-09-00, GIET leg.; 1♀: El Hierro, JN-C/CO-2523, Cueva de Jinama, 9-II-2000, GIET leg.; 1♀: El Hierro, Fi-VG/CO-2346, Cueva de Fileba, 8.II.2000, GIET leg. (DZUL, MCNT, cOro); 1♂: El Hierro, Fi-C/CO-2103, Cueva de Fileba, 1.II.2000, GIET leg. (cAss); 1♂ [teneral]: El Hierro, Cueva de Fileba, 4-XI-01, H.López leg. (cAss); 1♂ [remains; in ethanol]: El Hierro, Cueva de Jinama, 26.IX.00, JN-C/CO-3779, GIET leg. (DZUL); 1♀ [remaines; in ethanol]: NO: FI-C/CO-3868, El Hierro, Cueva de Fileba, Fecha: 15.IX.00, GIET leg. (DZUL); 1♀: No: FI-C/CO-5717, El Hierro, Cueva de Fileba, Fecha: 28/07/01, leg. S. de la Cruz (cAss).

Diagnosis: 5.0-6.8 mm. Habitus as in Fig. 38. Coloration of whole body more or less uniformly reddish brown, with the elytra, the legs, and the antennae yellowish brown.

Head distinctly oblong, 1.10 - 1.15 times as long as wide; widest at a short distance behind eyes, i.e. at slightly tapering posteriad (Fig. 39); eyes reduced: rudiments without pigmentation and without distinct ommatidia, in dorsal view about 1/5 - 1/6 the length of temples; integument with very dense, fine, shallow, non-areolate puncturation; interstices with distinct microsculpture. Antennae long and slender; antennomere III approximately 4 times as long as wide and distinctly longer than II; IV shorter than III and more than twice as long as wide; IV - X of gradually decreasing length; X approximately as wide as long (Fig. 39).

Pronotum 1.05 - 1.10 times as wide as long and about 0.95 times as wide as head; microsculpture distinct, rendering the extremely fine puncturation almost invisible (Fig. 39).

Elytra approximately 1.1 times as wide and at suture about as long as pronotum; puncturation very dense, fine, and weakly granulose. Hind wings of reduced length, about twice as long as elytra. Legs long and slender; metatarsomere I 4 - 5 times as long as wide; I - IV of decreasing length, IV weakly oblong (Fig. 41); protarsus with pronounced sexual dimorphism.

Abdomen with very fine and dense puncturation; posterior margin of tergite VII with narrow palisade fringe.

♂: protarsomeres strongly transverse and cordiform (Fig. 40); posterior margin of sterniteVII broadly concave, laterally with combs of about 10 palisade setae and on either side of middle with tuft of long black setae (Fig. 42); sternite VIII not distinctive (Fig. 43); aedeagus as in Figs. 44 - 45.

♀: protarsomeres weakly transverse and not cordiform.

Etymology: The name (Lat.) is a noun in apposition and means cave inhabitant.

Comparative notes and systematics: *Medon antricola* is readily identified by external characters alone, especially the large size, uniformly light coloration, the reduced eyes, long antennae and legs, the oblong head, as well as by the puncturation and microsculpture of the head and pronotum. Based on the evident similarities in the shape and chaetotaxy of the male sternite VII, the morphology of the aedeagus, the oblong head, as well as on the puncturation and microsculpture of head and pronotum, *M. antricola* is doubtlessly the sister species of *M. subcoriaceus*. It is not closely allied to *M. feloi*, another cave-dwelling species from the Canary Islands (see section 3.25).

Distribution and bionomics: The species is endemic to El Hierro, Canary Islands, where it was found at least in two caves, the Cueva de Jinama and the Cueva de Fileba in the north of the island. Larvae possibly belonging to this species were also found in caves in the south of El Hierro (P. OROMÍ, La Laguna, pers. comm. 2003). As can be inferred from the adaptive reductions of the eyes, wings, and pigmentation, as well as from the conspicuously long antennae and legs, *M. antricola* is a true troglobite. This is also supported by the circumstances of collection: the type specimens were found by handsampling (on bare ground) and with pitfall traps in the deep and dark parts of the caves, partly near water (P. OROMÍ, La Laguna, pers. comm. 2003). One specimen taken in November is teneral.

3.8. *Medon castaneus* (Gravenhorst, 1802)
(Figs. 46-52, Map 6)

Paederus castaneus Gravenhorst, 1802 (GRAVENHORST 1802: 60).

Lathrobium brevicorne Latreille, 1804 (LATREILLE 1804: 342).

Paederus quadratus Beck, 1817 (BECK 1817: 25).

Medon ruddii Stephens, 1833 (STEPHENS 1833: 273).

Types examined: *P. castaneus*: Lectotype ♂, present designation: 6361 / castanea Er., Paederus Gr. / Syntypus Lathrobium castaneum Gravenhorst 1802, labelled by Zool. Mus. Berlin, 7.2003 / Hist.-Coll. (Coleoptera) Nr. 6361 Lathrobium castaneum Gravenhorst, 1802, Europa, Zool. Mus. Berlin / Lectotypus ♂ *Paederus castaneus* Gravenhorst, desig. V. Assing 2003 / Medon castaneus (Gravenhorst) det. V. Assing 2003 (MNHUB). Paralectotype ♀: Syntypus Lathrobium castaneum Gravenhorst 1802, labelled by Zool. Mus. Berlin, 7.2003 / Hist.-Coll. (Coleoptera) Nr. 6361 Lathrobium castaneum Gravenhorst, 1802, Europa, Zool. Mus. Berlin / Paralectotypus ♀ *Paederus castaneus* Gravenhorst, desig. V. Assing 2003 / Medon castaneus (Gravenhorst) det. V. Assing 2003 (MNHUB).

Material examined (total: 92 exs.):

Portugal: 1 ex., Serra de S. Marmede, Marvao, 39°24N, 07°23W, 665 m, swept from vegetation, 16.III.2002, leg. Meybohm (cAss); 1 ex., Castelo Branco, S Manteigas, 1450 m, 16.IV.1960, leg. Besuchet (cSch).

Spain: 1 ex., Castilla-León, Segovia, San Rafael, 14.V.1960, leg. Comellini (cBor).

France: 1 ex., Gironde, Vendays-Montalivet, IX.1950, leg. Tempère (MHNG); 1 ex., Gironde, Pessac (MHNG); 1 ex., Poutou-Charentes, St. Georges-de-Didonne, VIII.1925 (MHNG); 1 ex., Rhône-Alpes, Ardéche, Saint-Agrève, 900m, III.1934, leg. Gaudin (UCBA, cZan); 1 ex., Lyon, 6.IV.1950 (MHNG); 1 ex., Alsace, Strasbourg, X.1953 (MHNG). **Locality not identified or ambiguous:** 1 ex., Ft. de St. Germain, I.1932, leg. Tempère (MHNG); 1 ex., St. Germain, 24.I.1937, leg. Levasseur (MHNG).

England: 1 ex., Surrey, Pyrford, 26.II.1992, leg. Owen (cOwe).

Sweden: 2 exs., Skåne, N Landskrona, Ålabodarna, vole burrow, 21.V.1971 & 25.V.1975, leg. Gillerfors (cGil).

Germany: Nordrhein-Westfalen: 1 ex., Münster, Gasselstiege, III.1991, leg. Feldmann (cFel). **Rheinland-Pfalz:** 1 ex., Landau, Rülzheim, meadow, mole nest, II.1987, leg. Persohn (cKöh). **Schleswig-Hostein:** 1 ex., Krummesse, 22.III.1973 (MHNG). **Niedersachsen:** 2 exs., Hannover, Herrenhäuser Gärten, 24.III.1988, leg. Assing (cAss); 1 ex., Hannover-Ahlem, fallow area, pitfall trap, 5.V.1992, leg. Sprick (cAss); 1 ex., Harz, Herzberg, pitfall trap, 5.V.1992 (cAss); 2 exs., Hann.-Münden, left bank of Fulda river, 6.I.1932, leg. Kirch (cSch); 2 exs., Holzminden, leg. Gerhard (NHMW). **Hessen:** 2 exs., Seeheim-Jugenheim, fallow, mole nest, II.2003, leg. Hetzel (cFel); 1 ex. [teneral], Karlshafen, 27.I.1934, leg. Folwaczny (MHNG); 2 exs., Erlensee, 10.II.1993, leg. Höhner (cKöh). **Bayern:** 1 ex., Bamberg, leg. Weise (NHMW). **Brandenburg/Berlin:** 1 ex., Frankfurt/O., Markendorf, Helenesee, 22.IV.1984, leg. Gasche (cSch); 4 exs., W Potsdam, Wildpark Golm, mole nest, coll. Neresheimer (DEI); 1 ex., Hönow, mole nest, coll. Neresheimer (DEI); 1 ex., Mittenwalde, mole nest, coll. Neresheimer (DEI); 10 exs., Strausberg, mole nest, coll. Neresheimer (DEI); 1 ex., NSG Rietzer See, 52°23N, 12°41E, Helsberg, rabbit burrow, fish bait, 16.V.1979, leg. Uhlig (DEI). **Sachsen:** 1 ex., Leipzig, 19.X.1913, leg. Linke (MHNG); 1 ex., Leipzig, Dölzig, leg. Linke (NHMW).

Austria: Vorarlberg: 2 exs., Feldkirch (NHMW). **Tirol:** 1 ex., Innsbruck, 4.XII.1932, leg. Pechlaner (NHMW); 1 ex., Innsbruck, leg. Strupi (MHNG). **Oberösterreich:** 1 ex., Ostermiething, mole nest, leg. Leeder (NHMW). **Niederösterreich/Wien:** 1 ex., Oberwaltersdorf, mole nest, leg. Franz (NHMW); 2 exs., Wien, Lobau, mole nest, 21.III.1926, leg. Breit (NHMW); 1 ex., Moosbrunn, mole nest, 1.III.1927, leg. Breit (NHMW); 3 exs., Wien, leg. Schade (NHMW, cAss); 12 exs., Purgstall, mole nests, 14.II.1957, 1.IV.1958, 13.XII.1958, 4.III.1959, 31.III.1959, 29.IX.1959, 4.X.1959 (3 exs.), 5.I.1959, 4.VII.1960, 20.X.1960, leg. Ressl (NHMW); 1 ex., Oberweiden, 11.II.1968, leg. Gotz (NHMW). **Burgenland:** 1 ex., Salmannsdorf (NHMW); 1 ex., Zurndorf, leg. Franz (NHMW).

Italy: Trentino-Alto Adige: 1 ex., Bressanone, 24.V.1957, leg. Peez (cBor); 1 ex., Bressanone, 2.III.1953, leg. Peez (cZan); 1 ex., Piemonte, Novara, Invorio, III.1971, leg. Rosa (cZan).

Czech Republic: 1 ex., Bohemia, Hostivice (MHNG); 1 ex., Prag (NHMW).

Poland: 1 ex., Lubin, 6.II.1916 (NHMW).

Slovakia: 3 exs., Banská Bystrica, XI.1923, leg. Roubal (MHNG, cBor).

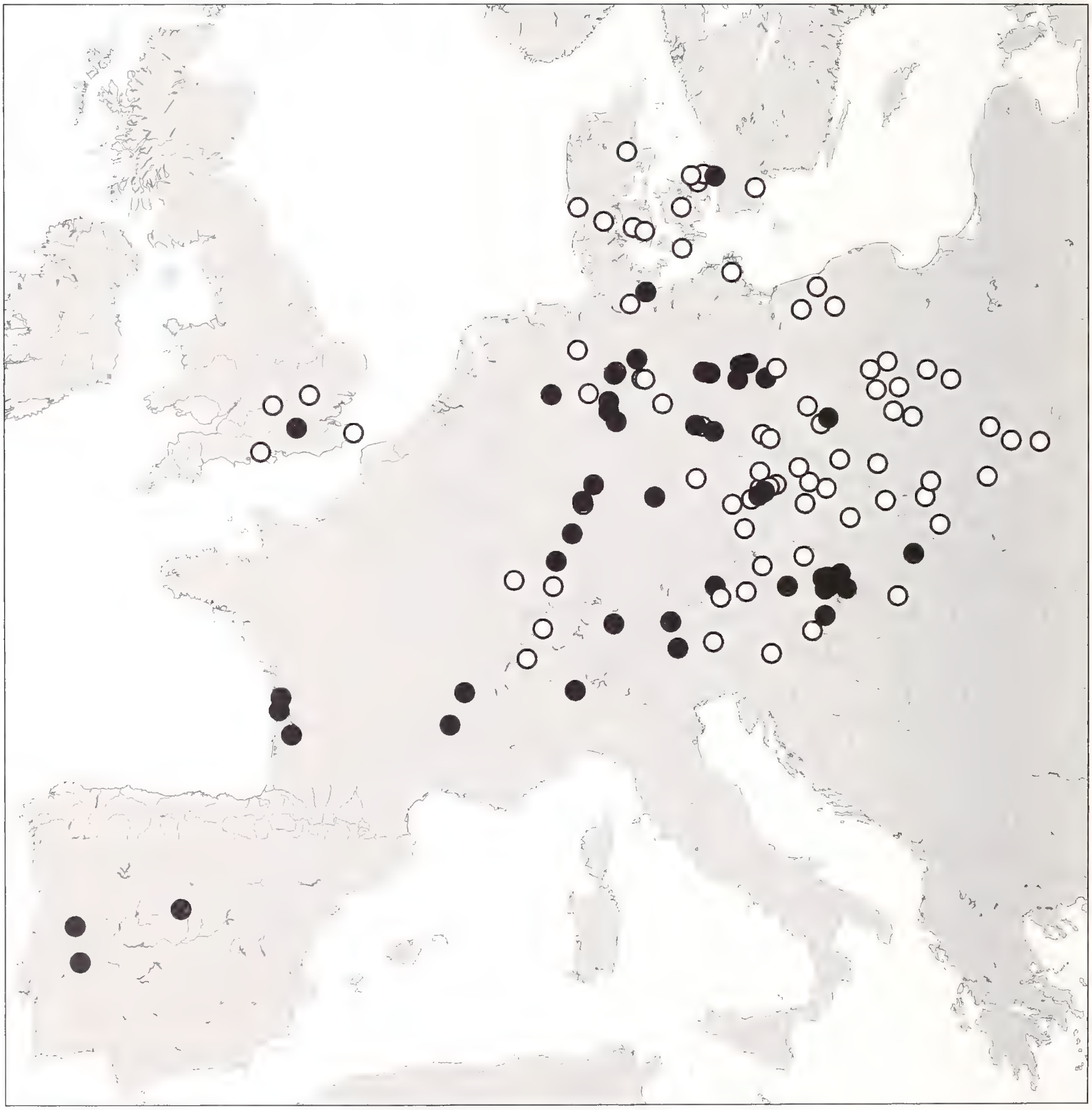
Locality illegible or not specified: 1 ex., 16.X.1960 (MHNG); 2 exs. (MHNG).

Comments: The original description of *Paederus castaneus* is based on an unspecified number of type specimens, so that the two types found in the historical collection of the MNHUB are attributed syntype status. In order to stabilize the present interpretation of the species, the male syntype is here designated as the lectotype.

Diagnosis: Large species, 6.0-8.0 mm. Habitus as in Fig. 46. Head dark brown to blackish brown, sometimes with the frons ferrugineous; pronotum dark brown to blackish, with the margins and especially the anterior angles more or less extensively ferrugineous; elytra rufous to castaneous; abdomen dark brown to blackish, with the apex, paraterga, and the tergal hind margins lighter; legs and antennae rufous.

Head at least weakly oblong and of subquadrangular shape, i.e. with subparallel lateral margins and marked posterior angles; eyes less than half the length of postocular region in dorsal view; puncturation moderately coarse, well-defined, and dense, with the interstices much narrower than the punctures, in median dorsal area usually sparser and with shining interstices (Fig. 47); shallow microsculpture may be present in posterior and lateral areas. Antenna very long and slender, antennomere IV and V more than twice as long as wide (Fig. 46).

Pronotum as wide as long or weakly transverse, slightly to distinctly narrower than head; puncturation denser and less well defined than that of head, often partly confluent; interstices narrow, but more or less shining (Fig. 47).



Map 6: Distribution of *Medon castaneus* (Gravenhorst) based on revised (filled circles) and selected literature records (open circles).

Elytra 1.15-1.20 times as wide and at suture 1.05-1.18 times as long as pronotum (Fig. 46); puncturation dense and granulose, less coarse than that of head and pronotum. Hind wings fully developed. Legs very long and slender, metatarsus almost as long as metatibia; metatarsomere III at least about 3 times as long as wide.

Abdomen with very fine and dense puncturation and with microsculpture; posterior margin of tergite VII with palisade fringe.

♂: protarsomeres distinctly dilated, protarsomere II cordiform and wider than long; posterior margin of sternite VII distinctly concave and with two combs of palisade setae, each consisting of usually more than 10 setae (Fig. 48); aedeagus long and slender (Figs. 49-52).

♀: protarsomeres weakly dilated, protarsomere II not wider than long and not distinctly cordiform.

Comparative notes: *Medon castaneus* is easily distinguished from all its Western Palaearctic congeners, except for *M. procerus* (see the following section), especially by its large size, the elongate legs and antennae, and by the long and slender aedeagus.

Distribution and bionomics: *Medon castaneus* represents an Atlanto-Mediterranean element (Map 6), its distribution ranging from the western part of the Iberian Peninsula to southern England, southern Scandinavia, Poland, western Russia, Ukraine, Slovakia, and Hungary (material examined). For more records see e.g. BARANOWSKI (1977, 1979), BOHÁČ (1985), BRUGE et al. (2001), BÜCHE & ESSER (1999), DRUGMAND (1989), ERMISCH & LANGER (1933), FALCOZ (1914), FOWLER (1888), HANSEN (1996), HANSEN et al. (1995), HANSEN (1964), HORION (1965), KOCH (1968), KÖHLER (2000), KÖHLER & KLAUSNITZER (1998), LUNDBERG (1995), TERLUTTER (1995), and TRONQUET (2001). In Scandinavia, it is present only in Denmark and Skåne. According to HORION (1965), there are old records from Slovenia and Hungary, and also from Ukraine (Wolyns´ka Oblast, Kiev) and Russia as far east as Samara, but these require confirmation. SILFVERBERG (1992) reports the species from Lithuania. Confirmed records from Italy are only known from two localities in the north (material examined; OSELLA & ZANETTI (1974)); it is also indicated from Lazio (southern Italy) (CICERONI & ZANETTI 1995; LUIGIONI 1929; PORTA 1926), but this old record has not been confirmed and should be considered doubtful.

Medon castaneus is nidicolous and usually associated with the nests and burrows of the European mole (*Talpa europaea* Linné), which, however, is absent from the western Iberian Peninsula. Thus, *M. castaneus* may also inhabit the nests of *Desmana pyrenaica* (Geoffroy Saint Hilaire) or *Talpa caeca* (Savi), which occur in this region. The observation that the species has also been found in rabbit burrows on two occasions, once on fishbait (material examined; BARANOWSKI (1979)), and once in vole burrows suggests that the host spectrum may also include other mammals with subterranean nests and burrows.

Nests of moles are inhabited by rather many species of Coleoptera and are relatively easy to find and to dig up, which is why there are numerous thorough studies on the beetle fauna of this habitat (e.g. HEINEMANN 1910; HORION 1933; NOWOSAD 1990; OSELLA & ZANETTI 1974; STROUHAL & BEIER 1928). According to these investigations, *M. castaneus* is rather rarely found in most regions. In the environs of Braunschweig (Germany: Niedersachsen), HEINEMANN (1910) found only 2 specimens in 225 nests. In the surroundings of Wien, STROUHAL & BEIER (1928) dug up 118 nests and collected 21 beetles. The by far most comprehensive and systematic study of the staphylinid fauna of mole nests was carried out in Poland by NOWOSAD (1990), who recorded *M. castaneus* in only 28 nests (48 specimens) of a total of about 5000 nests studied.

The literature data on the preferred biotope are diverse or even contradictory. According to most authors (e.g. JOY 1932; HORION 1933, 1965; STROUHAL & BEIER 1928; VOGT 1956), *M. castaneus* is usually found in damp situations, especially near rivers and streams, whereas LINKE (1927) reports it from dry places; on one occasion he found 14 specimens in a single nest.

Adult beetles have been found almost throughout the year, except in August. The low number of summer records, however, may also be due to the probably low number of nests examined during this period. Larvae have been found in July (BOHÁČ 1985, HORION 1965). A teneral adult was collected in January (material examined). One specimen was swept from vegetation in March (Portugal) and two specimens were caught with pitfall traps in April and at the beginning of May, suggesting that dispersal by flight and on the ground probably takes place in early spring.

3.9. *Medon procerus* (Perez Arcas, 1874), sp. propr. (Figs. 53-57)

Lithocharis procera Perez Arcas, 1874 (PEREZ ARCAS 1874: 114ff).

Material examined: Spain: 2 exs., Madrid, Cueva de la Magdalena (NHMW, cAss).

Diagnosis: Largest species of the genus in the Western Palaearctic region, 7.0-9.0 mm (Fig. 53). Coloration uniformly ferrugineous.

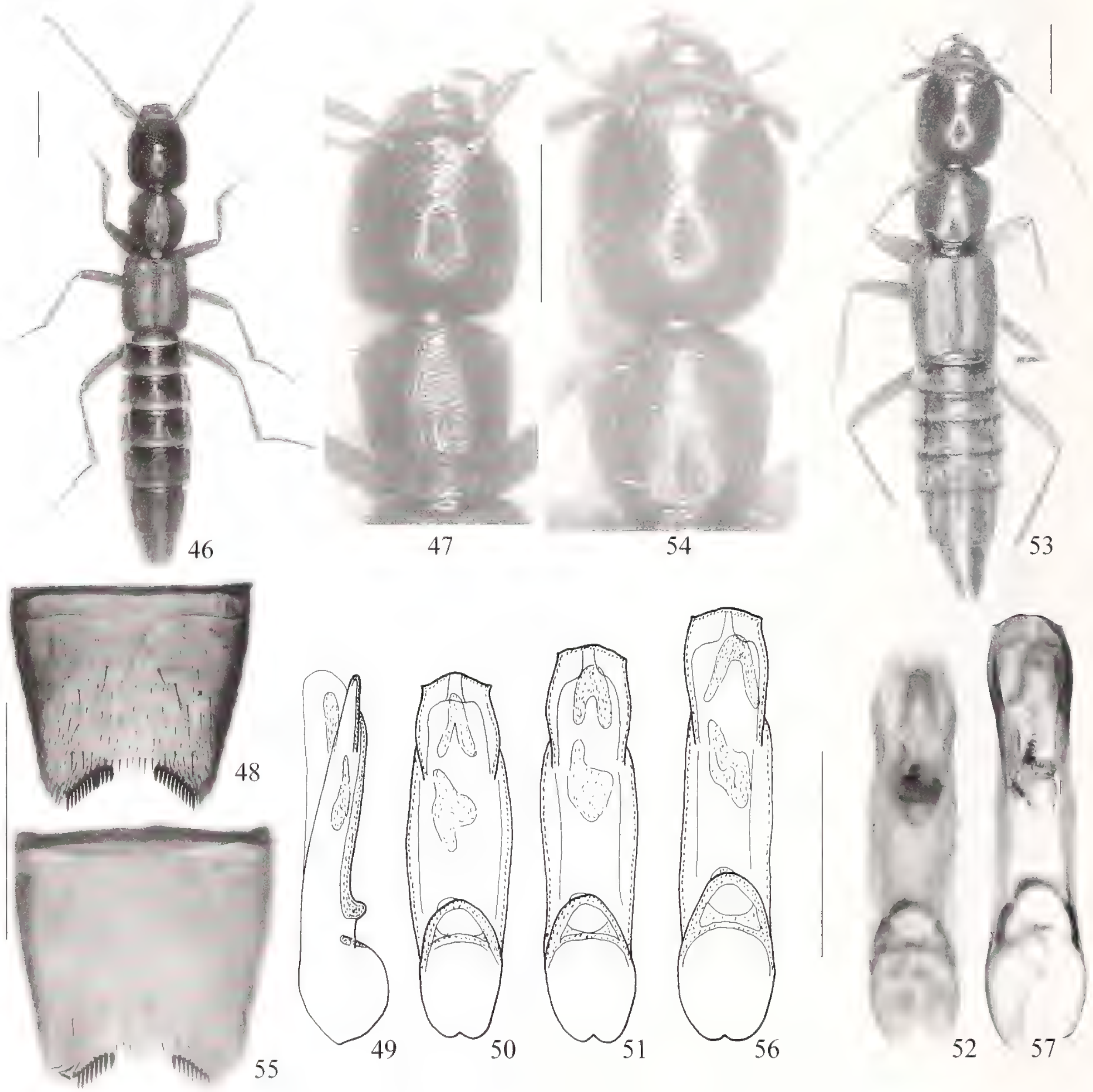
Head very large and of ellipsoid shape, i. e. lateral margins convex and posterior angles almost obsolete; eyes slightly smaller than in *M. castaneus*; puncturation as in

M. castaneus, but slightly less coarse (Fig. 54). Antennae of similar morphology as in *M. castaneus*.

Pronotum small in relation to head, distinctly tapering posteriad; puncturation less dense and more well defined than is usually the case in *M. castaneus* (Fig. 54).

Legs even longer and more slender than in *M. castaneus*; length of metatibia 1.7-1.8 mm (maximum length in largest specimens of *M. castaneus* 1.4 mm). Elytra and abdomen as in *M. castaneus* (Fig. 53).

♂: protarsomeres I - IV distinctly dilated; sternite VII of similar morphology and chaetotaxy as in *M. castaneus*, but more oblong and posterior concavity shallower in relation to total length of sternite (Fig. 55); sternite VIII elongate and slender; aedeagus longer than in *M. castaneus* and with longer and more slender ventral process (Figs. 56-57).



Figs. 46-57. *Medon castaneus* (Gravenhorst) (46-52) and *M. procerus* (Perez Arcas) (53-57): Habitus (46, 53); head and pronotum (47, 54); male sternite VII (48, 55); aedeagus in lateral and in ventral view (49-57; 49, 50: northern Germany; 51, 52: Portugal). Scale bars: 46-48, 53-55: 1.0 mm; 49-52, 56-57: 0.5 mm.

Comparative notes: The species is distinguished from the similar *M. castaneus* especially by the uniformly ferrugineous coloration, the ellipsoid shape of the head, the longer legs, and the longer and more slender aedeagus. From all other Western Palaearctic congeners, it is readily separated by its much greater body size alone.

Comments: The types of this species were not examined, but in view of the distinctive external appearance and the fact that the non-type specimens listed above were collected at the type locality, there is no doubt that the present interpretation is correct. *M. procerus* was previously regarded as a synonym of *M. castaneus* (e.g. COIFFAIT 1984). However, the constant differences in external morphology, in the shape of the primary and secondary sexual characters, as well as the different habitat suggest that it represents a distinct species. A similar case of adelphotaxa, one of them widespread and the other an endemic troglobite, is known from the Eastern Mediterranean (ASSING 2004a): *Medon fusculus* and *M. dobrogicus* Decu & Georgescu.

Distribution and bionomics: This troglobite is known only from the Cueva de la Magdalena, a cave near Madrid, where it is apparently endemic. According to PEREZ ARCAS (1874) adult beetles were found almost throughout the year.

3.10. *Medon pocofer* (Peyron, 1857) (Figs. 58-59)

Lithocharis pocofera Peyron, 1857 (PEYRON 1857: 718ff).

Lithocharis maritimus Aubé, 1863 (AUBÉ 1863: 36).

Material examined (total: 51 exs.; for additional material see ASSING (2004a))**:**

France: Provence: 2 exs., locality not specified (NHMW); 1 ex., Port Miod near Cassis, "feinkiesiger bis grobschottriger Untergrund", 10.VIII.1959, leg. Schuster (NHMW); 1 ex., Nice, III.1954 (cBor); 1 ex., Nice, 25.IX.1918 (MHNG); 10 exs., Nice, 5.III.1954 (MHNG, cAss); 2 exs., La Seyne (NHMW); 3 exs., Saint-Raphaël, leg. Fauvel (NHMW, cAss); 1 ex., Fréjus, VII.1892, leg. Rey (NHMW); 1 ex., Toulon, leg. Bauduer (NHMW); 1 ex., Toulon (DEI); 1 ex., Var, locality not specified (DEI); 1 ex., Var inundation [W Nice], Alpes Maritimes, IV.1859 (DEI); 1 ex., Antibes (DEI).

England: 1 ex., Dorset, Lulworth Cove, shingle, 22.III.1990, leg. Owen (cOwe).

Italy: Friuli-Venezia Giulia: 1 ex., Trieste, Sistiana, Adria, leg. Breit (NHMW); 1 ex., Trieste, Grignano, IX.1907, leg. Krekich (MHNG). **Liguria:** 7 exs., Genova, XII.1900, leg. Dodero (NHMW, cAss); 1 ex. [teneral], Genova, VII.1899, leg. Dodero (NHMW); 2 exs., Genova, III.1894, leg. Dodero (NHMW); 4 exs., Genova, IV.1893, leg. Dodero (DEI, cAss); 2 exs., Genova, I.1918, leg. Dodero (MHNG); 1 ex., Genova, XI.1918, leg. Dodero (NHMW); 4 exs., Genova, leg. Dodero, Hauser (DEI, NHMW). **Umbria:** 1 ex., locality not specified (NHMW).

Diagnosis: See ASSING (2004a). Habitus as in Fig. 58. All tarsomeres III and IV are transverse and more or less cordiform (Fig. 59), a character not emphasized by ASSING (2004a), but distinguishing *M. pocofer* from all other Western Palaearctic species.

Comments: The type material of *M. pocofer* was looked for, but not found, in the collections of the MNHNP. However, both the characters and the ecological details indicated in the original description leave no doubt that the present interpretation is correct.

Distribution and bionomics: According to the literature, *Medon pocofer* is distributed on the Atlantic coasts northwards to southern England and in the Western Mediterranean, including Algeria and Tunisia (COIFFAIT 1984; FOWLER 1888; NORMAND 1935). The easternmost record is from Montenegro (ASSING 2004a). In the Western Mediterranean, I have seen material only from southern France (Provence) and Italy. LUIGIONI (1929) reports the species from various Italian regions (Liguria, Venezia Giulia, Lazio, Sardinia, and Sicily) and from Corsica. Based on the material examined, the species is not rare at the coasts of Var, Alpes Maritimes, and Liguria.

Among Western Palaearctic *Medon* species *M. pocofer* is the only representative that is apparently confined to coastal habitats. It is usually found under seaweed and under stones between shingles (COIFFAIT 1984; FOWLER 1888; JOY 1932; NORMAND 1935). FOWLER (1888) observes that the specimens are very quick and immediately hide between shingles when disturbed. One specimen collected in July was teneral (material examined).

3.11. *Medon rufiventris* (Nordmann, 1837) (Figs. 60-61, Map 7)

Lathrobium rufiventre Nordmann, 1837 (NORDMANN 1837: 147f).

Medon anatolicum Coiffait, 1970a (COIFFAIT 1970a: 704ff); synonymy by ASSING (2004a).

Medon burdigalensis Coiffait, 1970a (COIFFAIT 1970a: 711f) **syn. n.**

Medon aquitanicum Coiffait, 1970a (COIFFAIT 1970a: 712) **syn. n.**

Medon siculum Coiffait, 1970a (COIFFAIT 1970a: 709ff) **syn. n.**

Medon sicilianum Coiffait, 1970c (Coiffait 1970c: 712); replacement name for *M. siculus* Coiffait; **syn. n.**

Types examined: *M. burdigalensis*: Holotype ♂ [aedeagus missing]: Gironde V.45, Gazinet, H. Coiffait / MUSEUM PARIS COLL H. COIFFAIT / HOLOTYPE / Medon burdigalensis Coiff. H. COIFFAIT det. 1969 / Medon rufiventris (Nordmann) det. V. Assing 2003 (MNHNP).

M. aquitanicus: Holotype ♂: Gironde, Cussac / Collection H. Coiffait / MUSEUM PARIS COLL H. COIFFAIT / HOLOTYPE / Medon aquitanicum Coiff. H. COIFFAIT det. 1969 / Medon rufiventris (Nordmann) det. V. Assing 2003 (MNHNP).

M. siculus: Holotype ♂: U. Lostia, Sardinia / MUSEUM PARIS COLL H. COIFFAIT / HOLOTYPE / Medon siculum Coiff. H. COIFFAIT det. 1969 / Medon rufiventris (Nordmann) det. V. Assing 2003 (MNHNP).

M. anatolicus: Holotype ♂: Turquie (Isparta), Bodemli, H. Coiffait, 27.V.54 / HOLOTYPE / Medon anatolicum Coiff. H. COIFFAIT det. 1969 (MNHNP). Paratypes: 1♂, 1♀: same data as holotype (MNHNP).

Comments: According to Coiffait (1970a), *M. burdigalensis* is distinguished from *M. rufiventris* by the finer puncturation of the pronotum and by the different shape of the aedeagus. The puncturation of the pronotum is indeed very fine in the holotype, but this character is highly variable in the species and I have seen specimens with a similarly punctured pronotum also from other parts of the range of *M. rufiventris*, e.g. from Greece. The aedeagus of the holotype is apparently lost, but the drawing provided in the original description is quite in agreement with the aedeagus of *M. rufiventris*. The apical emargination is rather small, but this is probably an artefact resulting from mounting a dry aedeagus. The fact that the illustration of the aedeagus of *M. rufiventris* in Coiffait (1984: 19, figs. 6I and 6J) is taken from the literature suggests that Coiffait had not seen a male *M. rufiventris* himself.

In the original description of *M. aquitanicus*, Coiffait (1970a) states that the species is similar to *M. burdigalensis*, but separated by the more parallel shapes of the head and pronotum, by the more numerous black palisade setae at the posterior margin of the male sternite VII, the lower distance between the two clusters of palisade setae, and by the different shape of the aedeagus. Head shape is an extremely variable character in *M. rufiventris*; the majority of specimens have a relatively large and somewhat wedge-shaped head, but the head may also be of subparallel shape and/or of reduced size (Assing 2004a). The apex of the aedeagus (Fig. 61) differs somewhat from the usual condition encountered in *M. rufiventris*, but teratological aedeagi are a common phenomenon in the genus.

Neither the male secondary sexual characters nor the other external characters of the holotypes of *M. burdigalensis* and *M. aquitanicus* (Fig. 60) provide sufficient evidence that these specimens should represent distinct species (not to mention the unlikelihood of endemic *Medon* species occurring in Gironde), so that both *M. burdigalensis* and *M. aquitanicus* is here placed in the synonymy of *M. rufiventris*.

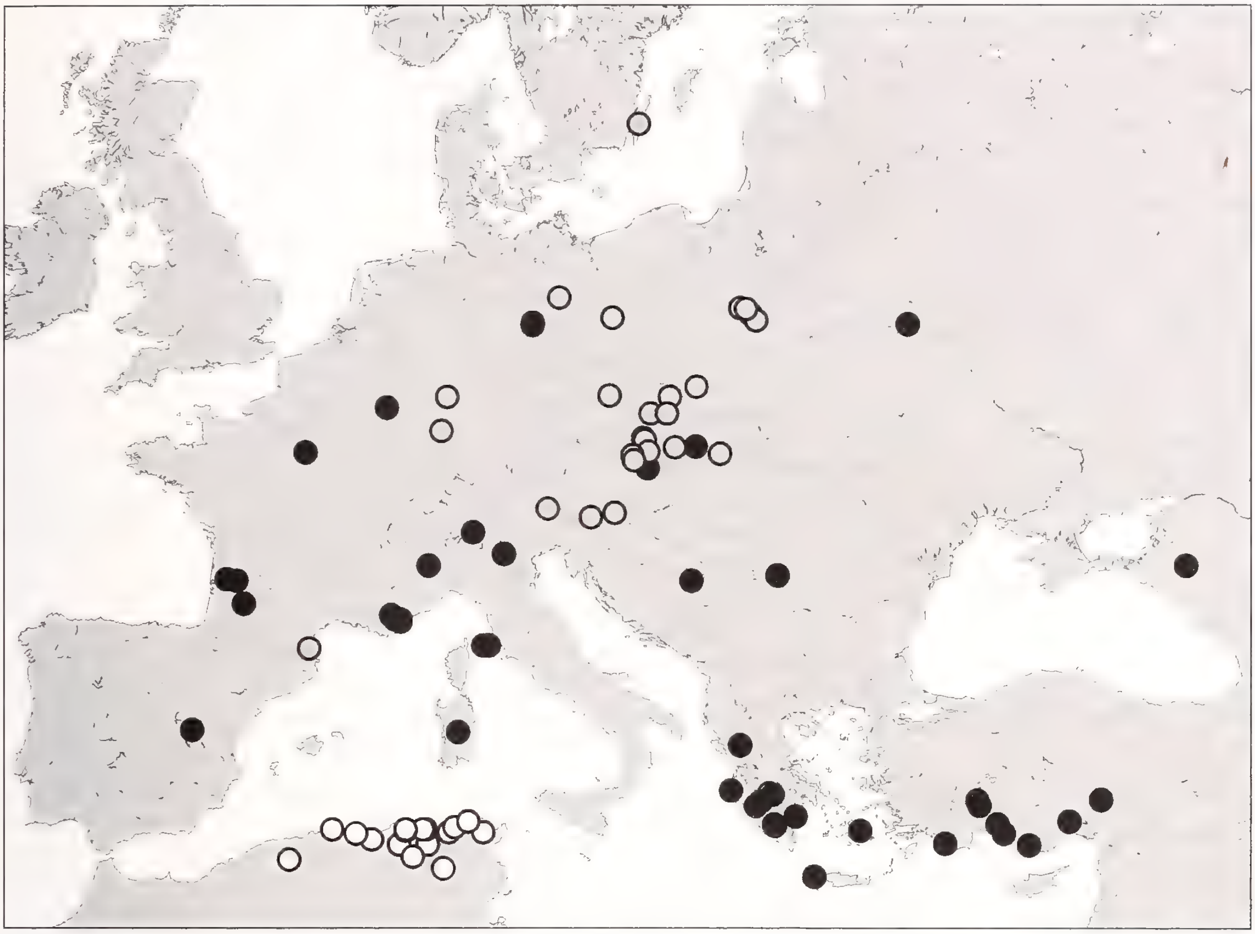
The type locality indicated in the original description of *M. siculus* ("Sicile") is clearly incorrect; the label attached to the holotype gives "Sardinia". This error has resulted in the conclusion that *M. siculus* (later known under the replacement name *M. sicilianus*) is endemic to Sicily (Coiffait 1984; Ciceroni & Zanetti 1995). Coiffait (1970a) compares *M. siculus* with *M. brunneus*, probably because of the relatively coarse puncturation of the pronotum of the type specimens, but an examination of the holotype revealed that it is conspecific with the senior name *M. rufiventris*. The puncturation of the pronotum and of the head is indeed coarser than is usually the case in the species, but, like the size and the shape of the head, the puncturation of the forebody is subject to pronounced intraspecific variation in this species and the condition found in the holotype is still within the range observed in *M. rufiventris*. An examination of other characters, including the male secondary sexual characters and the morphology of the aedeagus, did not produce any evidence that the types of *M. siculus* should represent a distinct species.

Based on non-type material and the original description (Coiffait 1970a), the synonymy of *M. anatolicus* with *M. rufiventris* was already established by Assing (2004a). A recent examination of the types of *M. anatolicus* confirms this synonymy.

Additional material examined (total: 48 exs.; for additional material see Assing (2004a))**:**

Spain: 1 ex., Cuenca, Serrania de Cuenca, 40°07N, 02°02W, 17.V.2002, leg. Starke (cAss).

France: 2 exs., Landes, Sos (NHMW); 2 exs., Île-de-France, Fontainebleau, IV.1904, leg. Mequignon (MHNG); 1 ex., Fontainebleau, leg. Mequignon (MHNG); 1 ex., Fontainebleau, 20.III.1905, leg. Gruardet (MHNG); 1 ex., Var, St.-Paul-en-Forêt, 5.I.1939 (MHNG); 4 exs., Var, Figanières, 29.IV.1975, leg. Zoia (UCBA, cZan); 2 exs., Var, Bagnols-en-Forêt, cork tree, IV.1937 (MHNG); 2 exs., Var, Plan de Canjuers, 43°42N, 06°18E, 22.IV.1954 (MHNG); 1 ex., Var, locality not specified, II.1950 (MHNG).



Map 7: Distributions of *Medon rufiventris* (Nordmann) (black circles: revised records; grey circles: selected literature records) and of *M. africanus* (Fauvel) (white circles; examined records only).

Luxemburg: 1 ex., locality not specified, leg. Franz (cAss).

Italy: 1 ex., Lombardia, Berbenno di Valtellina, Colorina, 4.IV.1972 (cZan); 1 ex., Piemonte, Brandizzo, mole nest, 28.XII.1973, leg. Osella (cZan); 1 ex., Veneto, Grezzana (VR), 10.IV.1992, leg. Zanetti (cZan); 1 ex., Elba, 22.-31.V.1993, leg. Rauhut (cAss); 7 exs., Elba, Mt. Capanno, 600 m, under chestnut bark, 30.III.-13.IV.1921, leg. Moczarski & Scheerpeltz (NHMW, cAss).

Germany: 1 ex., Sachsen-Anhalt, Dessau, leg. Nebel (NHMW).

Slovakia: 1 ex., Hronská Breznica [48°34N, 19°00E], leg. Roubal (MHNG).

Greece: 11 exs., Métsovon, 1200 m, 8.IV.1993, leg. Frisch (MNHUB, cAss); 4 exs., Pelopónnisos, Olympia, Ladzoi, 100 m, 25.III.1992, leg. Frisch (MNHUB, cAss); 1 ex., Pelopónnisos, Taygetos, Katafigion, 1550 m, 10.IX.1995, leg. Zoia (cZan).

Belarus: 1 ex., Gomel region, Simonitschi, National Park "Pripiatsky", 20.VII.1998, leg. Sheshurak (cGon).

Diagnosis: See ASSING (2004a).

Distribution and bionomics: Based on the material examined, *M. rufiventris* is evidently a Ponto-Mediterranean element, its distribution ranging from eastern Anatolia, Krasnodar, and Belarus in the southeast and east to the central parts of Poland and Germany and to Luxemburg in the north, and finally to western France, and northeastern Spain in the west (material examined). There is an isolated record from the Swedish island Öland, the only Scandinavian locality known for the species (LUNDBERG 1995). For additional records see BOHÁČ (1985), HORION (1965), KÖHLER (2000), KÖHLER & KLAUSNITZER (1998), LUNDBERG (1995), SCHEERPELTZ (1968), SZUJECKI (1968), and TRONQUET (2001). The species is here recorded from Luxemburg for the first time. It is unknown from the British Isles (LOTT & DUFF 2003), Belgium (BRUGE et al. 2001), and from the Baltic countries (SILFVERBERG 1992). Rather recent German records are from Berlin and Sachsen-

Anhalt (KORGE 1989; SCHÜLKE 1998). The presence of the species in Sardinia was considered doubtful by CICERONI & ZANETTI (1995), but is here confirmed through the holotype of *M. siculus* Coiffait. In view of the general distribution pattern of the species, as well as of the absence of any confirmed records, the presence of the species in Northwest Africa, as indicated by COIFFAIT (1984) and HORION (1965), must be considered most unlikely. Previous records from this region are evidently based on confusion with other species, especially the externally similar *M. africanus*.

Medon rufiventris was mostly found associated with dead wood, especially in or under bark of old or dead tree trunks of deciduous trees (various species of oak, beech, chestnut) and pine trees (material examined; see also ASSING (2004a), HORION (1965), KORGE (1989), and VOGT (1968)). One specimen was collected from a mole nest (OSELLA & ZANETTI 1974; specimen examined). The examined beetles (see also ASSING 2004a) were collected during the period from December through July, and in October, the vast majority of them in spring (March through June). One of three specimens taken in October was teneral (ASSING 2004a).

3.12. *Medon africanus* (Fauvel, 1872)
(Figs. 62-69, Map 7)

Lithocharis africana Fauvel, 1872 (FAUVEL 1872: 38).

Medon bodemeyeri Bernhauer, 1915 (BERNHAUER 1915: 266) **syn. n.**

Types examined: *L. africana*: Lectotype ♂, present designation: Bône / africanus Fvl. type / Coll. et det. A. Fauvel Medon rufiventris Nordm. R.I.Sc.N.B. 17.479 / TYPE / Medon africanus (Fauvel) det. V. Assing 2003.

M. bodemeyeri: Lectotype ♀: Ain Draham, Tunis, B. V. Bodemeyer / Bodemeyeri Bernh. Typus / Chicago NHMus, M. Bernhauer Collection / Lectotypus *Medon bodemeyeri* ♀ Bernhauer desig. V. Assing 2003 / Medon africanus (Fauvel) det. V. Assing 2003 (FMNH); 1♀: same data, but "Cotypus ..." (FMNH); 3♀♀: same data, but without type labels (DEI, FMNH); 1♂: Ain Draham, Tunis, B. V. Bodemeyer / Syntypus / Medon Bodemeyeri Bernh. / O. Leonhard / Coll. DEI Eberswalde / Paralectotypus *Medon bodemeyeri* ♂ Bernhauer desig. V. Assing 2003 / Medon ripicola (Kraatz) det. V. Assing 2003 (DEI).

Comments: FAUVEL (1872) neither specified the number of types nor did he designate a holotype. Therefore, in order to fix the identity of *M. africanus*, the male syntype in the Fauvel collection is here designated as the lectotype.

The original description of *M. bodemeyeri* is based on an unspecified number of syntypes (BERNHAUER 1915). Five of them were found in the collections of the FMNH and the DEI; four of them – the ♀♀ – are conspecific with *M. africanus* (Fauvel), the male is conspecific with *M. ripicola* (Kraatz). The original description is in better agreement with the ♀♀, one of which was labelled as "Typus" by Bernhauer. In view of the fact that the type series consists of two species, a lectotype designation is mandatory. The female with Bernhauer´s type label was selected as the lectotype and *M. bodemeyeri* Bernhauer is placed in the synonymy of *M. africanus* (Fauvel).

Additional material examined (total: 51 exs.):

Tunisia: 1 ex., 2 km E Aïn Sobah, 18 km E Tabarka, 100 - 200 m, 1.X.1995, leg. Schulz & Vock (cAss); 3 exs., "Tunis" (NHMW); 1 ex., Aïn Draham (= Ayn ad Darahim; 36°47N, 8°42E) (cAss); 1 ex., same locality, 6.IV.1962, leg. Besuchet (MHNG); 1 ex., same locality, VI.1884 (IRSNB); 2 exs., ca. 2 km S Aïn Draham, 36°44N, 08°41E, 670 m, litter of oak forest, 28.XII.2004, leg. Assing (cAss); 2 exs., El Feidja (IRSNB); 11 exs., Aïn Soltane, near Ghardimaou, 30.IV.2004, leg. Lackner (cAss).

Algeria: 1 ex., Laverdure [=Mechroha], 7.X.1929, leg. Schatzmayr (FMNH); 6 exs., Bou Berak, Dellys (IRSNB, cSch); 2 exs., Bou Berak (IRSNB, NHMW); 1 ex., Grande Kabylie, Forêt d´Akfadou, Adekar, 1300 m, 15.V.1988, leg. Besuchet, Löbl & Burckhardt (MHNG); 2 exs., Annaba ['Bône'] (NHMW); 1 ex., Idügh [Edough] (MHNG); 2 exs., Constantine (MHNG, cAss); 1 ex., Mt. Babor (IRSNB); 1 ex., St. Antoine, leg. Thery (IRSNB); 1 ex., Theniet el Had ["Teniet el H."], cedar forest (IRSNB); 1 ex., Theniet el Had, 30.V.-5.VI.1954, leg. Fagel (IRSNB); 1 ex., Ain Babouche ["Babouch"] (IRSNB); 1 ex., Philippeville (IRSNB).

Locality not identified: 2 exs., Ternano (?) (MHNG).

Diagnosis: 3.7-5.0 mm. Habitus as in Figs. 62-63. Head, pronotum, and anterior segments of abdomen dark brown to blackish brown; elytra and abdominal apex rufous; legs and antennae ferrugineous.

Head (Figs. 64-65) approximately as wide as long or weakly oblong, of similar shape as in *M. cauchoisi*; eyes relatively large, clearly more than half the length of postocular region in dorsal view; puncturation dense, relatively coarse, and non-areolate; interstices mostly narrower, in central dorsal area often wider than punctures, usually without microsculpture.

Pronotum as wide as or slightly wider than head (Figs. 64-65); puncturation similar to that of head or slightly less coarse; microsculpture absent.

Elytra about 1.5 times as wide and at suture 1.15-1.20 times as long as pronotum; puncturation fine and dense. Hind wings fully developed.

Abdomen with fine and dense puncturation; posterior margin of tergite VII with palisade fringe.

♂: posterior margin of sternite VII distinctly concave and with two combs of about 10 or more palisade setae (Fig. 66); aedeagus with apex of ventral process of distinctive morphology (Figs. 67-69).

Intraspecific variation: The species is extremely variable, especially regarding the puncturation (size and density of punctures) of the forebody (Figs. 62-64).

Comparative notes: *Medon africanus* is most similar to *M. cauchoisi* and *M. rufiventris*. From the former, it is distinguished by the somewhat less coarse and less dense puncturation and the consequently more shining appearance of the head and pronotum, the relatively wider pronotum, the more convex posterior margin and the more numerous palisade setae of the male sternite VII, and by the different morphology of the aedeagus. *Medon rufiventris* often has a posteriorly dilated head, a finer and sparser puncturation of the head and pronotum, a male sternite VII with a usually slightly less strongly concave posterior margin and with on average fewer palisade setae, and an apically emarginate aedeagus (ventral view).

Distribution and bionomics: The species is currently known only from Tunisia and Algeria (Map 7). For additional Tunisian and Algerian localities see BORDONI (1988) and NORMAND (1935). Like *M. rufiventris*, *M. africanus* apparently lives under bark of deciduous and coniferous trees (NORMAND 1935; PEYERIMHOFF 1919). Two specimens from Tunisia were sifted from the leaf litter of an oak forest. The material with specified dates on the labels was found in April - June, October, and December.

3.13. *Medon vicentensis* Serrano, 1993 (Figs. 70-72)

Medon vicentensis Serrano, 1993 (SERRANO 1993: 4ff).

Material examined:

Madeira: 1 ex., São Vicente, Gruta dos Cardais, pitfall trap, 5.I.1996, leg. Erber (cErb).

Diagnosis: For a more detailed description see SERRANO (1993).

4.4-5.4 mm. Habitus as in Fig. 70. Coloration of whole body uniformly ferrugineous. Head large, approximately as wide as long; eyes reduced to minute rudiments, without ommatidia; puncturation distinct, moderately coarse and moderately sparse, interstices, except for the sparsely punctured dorso-median area, on average about twice as wide as punctures; surface with pronounced microreticulation and almost matt (Fig. 71). Antenna slender, antennomeres III - V more than twice as long as wide; VI about twice as long as wide; VII about 1.5 times as long as wide (Fig. 72).

Pronotum slightly narrower than head; approximately as wide as long; puncturation finer and less distinct than that of head, median line impunctate; microreticulation pronounced (Fig. 71).

Elytra widest near posterior margin, anterior external angles almost obsolete; as wide as or slightly narrower than pronotum; at suture about 0.7 times as long as pronotum; puncturation very fine, ill-defined and moderately dense; with much weaker microsculpture and much more shine than head and pronotum (Fig. 71). Hind wings completely reduced.

Abdomen with moderately dense, fine, slightly granulose puncturation; microsculpture present, but weaker than that of head and pronotum; posterior margin of tergite VII without palisade fringe.

♂: posterior margin of sternite VII of similar shape and chaetotaxy as in *M. dilutus*; aedeagus as illustrated by SERRANO (1993).

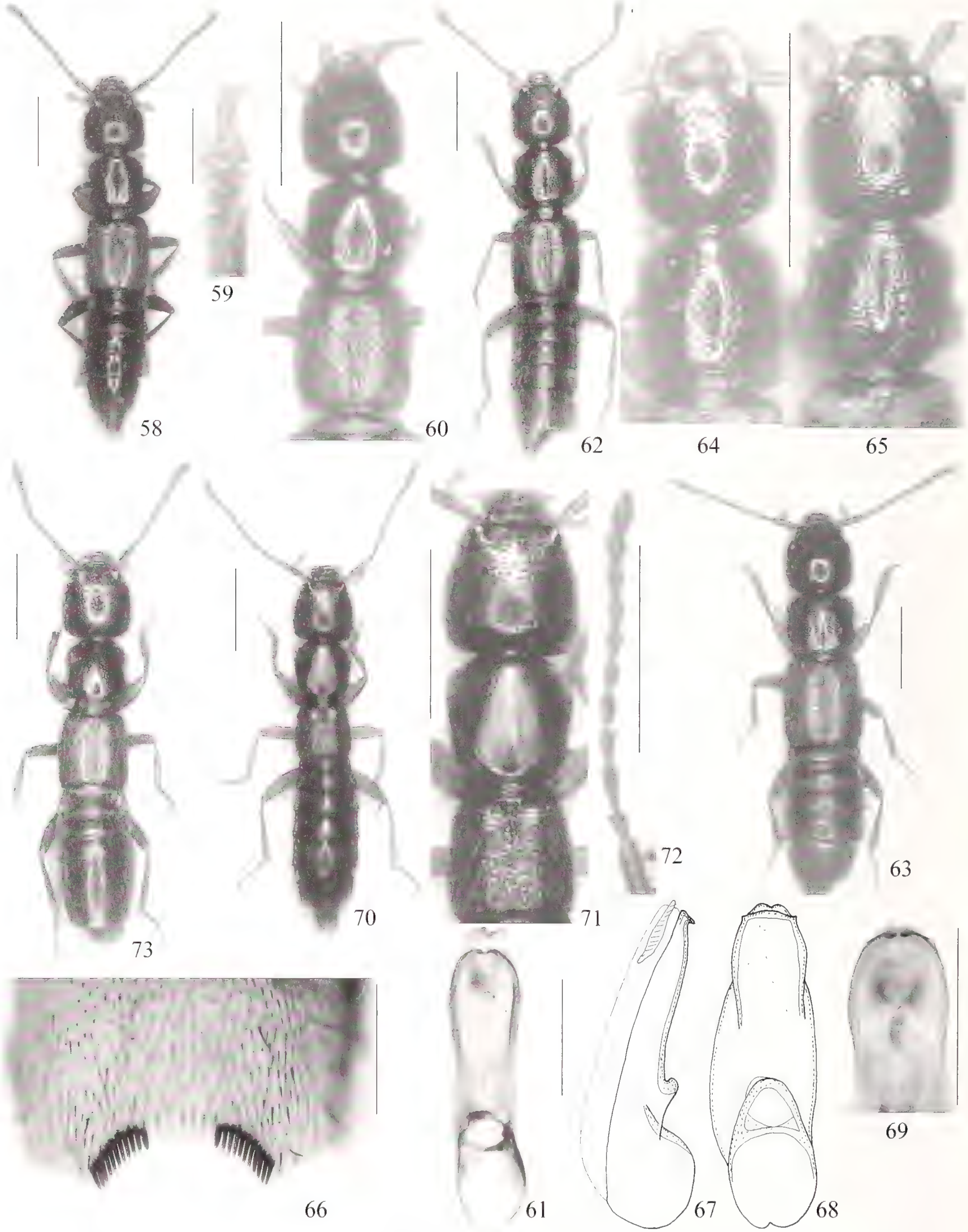
Comparative notes: This species is readily distinguished from its Western Palaearctic congeners by the almost completely reduced eyes, the long and slender antennae, the reduced pigmentation and wings, and by the male sexual characters. The only other troglobiont *Medon* species with almost completely reduced eyes, i. e. without ommatidia, in the Western Palaearctic are *M. feloi* from La Palma and *M. antricola* from El Hierro, Canary Islands. These species are also similar in the distinctly microreticulate and rather shallowly punctate head and pronotum. *Medon feloi*, however, has shorter antennae, a more convex (cross-section) and more oblong head, a more slender and posteriorly less distinctly tapering pronotum, longer elytra, not distinctly dilated protarsomeres I - IV, a differently shaped aedeagus, and its male secondary sexual characters are similar to those of *M. indigena*. *Medon antricola*, on the other hand, is distinguished by much greater body size, larger eye rudiments, longer and more slender legs and antennae, a much more oblong and posteriorly tapering head, and completely different male sexual characters.

Distribution and bionomics: *Medon vicentensis*, a true troglobite, is a local endemic of Madeira proper, where it is known only from a cave system near São Vicente.

3.14. *Medon augur* Fauvel, 1906 (Fig. 73)

Medon augur Fauvel, 1906 (FAUVEL 1906: 89).

Type examined: Holotype ♀: Corse / Croatie / augur Fvl.l / Ex-Typis / R. I. Sc.N.B. 17.479, Coll. et det. A. Fauvel (IRSNB).



Figs. 58-73. *Medon pocofer* (Peyron) (58-59), *M. rufiventris* (Nordmann) (holotype of *M. aquitanicus* Coiffait) (60-61), *M. africanus* (Fauvel) (62-69; 62: lectotype), *M. vicentensis* Serrano (70-72), and *M. augur* Fauvel (73, holotype): Habitus (58, 62, 63, 70, 73; 63: Algeria); protarsus (59); forebody (60, 71); head and pronotum (64, 65; 64: Algeria, 65: Tunisia); male sternite VII (66); aedeagus in lateral and in ventral view (61, 67, 68); apical part of aedeagus in ventral view (69); antenna (72). Scale bars: 58, 60, 62-66, 70-73: 1.0 mm; 59, 61, 67-69: 0.2 mm.

Comments: The original description is based on a holotype from Corsica ("Corse. – Unique") and an additional specimen from Croatia ("J´en ai vu un second exemplaire de Croatia") (FAUVEL 1906). The label "Croatie" attached to the pin of the holotype suggests that Fauvel apparently exchanged the Croatian specimen with a colleague, but kept the locality label and added it to the pin of the type specimen from Corsica. Types and other material with different locality labels attached to the same pin are not uncommon in the Fauvel collection (see e.g. ASSING 1999b).

It seems somewhat unlikely that the holotype is a representative of a distinct species with a distribution confined to Corsica. (The Croatian specimen attributed to this species in the original description probably refers to the similar *M. dilutus pythonissa* (Saulcy).) The holotype could be an extremely large specimen of *M. rufiventris*. However, it cannot be assigned to this nor any of the other widespread species without doubt, so that it is here maintained as a valid species, until males become available from Corsica.

Diagnosis: 4.8 mm. Habitus as in Fig. 73. Of similar general appearance as *M. dilutus pythonissa*. Head, pronotum, and abdomen (except apex and posterior margins of segments) dark brown; elytra, legs, and antennae ferrugineous.

Head large and convex, as wide as long; eyes relatively small (about as small as in *M. dilutus*), not distinctly projecting from lateral outline of head and slightly less than one third the length of temples in dorsal view; puncturation coarse (similar to *M. dilutus pythonissa* and *M. rufiventris*), along median line without or with very sparse puncturation; microsculpture absent.

Pronotum as wide as long, distinctly narrower than head; puncturation slightly less coarse than that of head; median line without punctures; microsculpture absent.

Elytra 1.13 times as wide and at suture 0.98 times as long as pronotum. Protarsomeres I - IV dilated (about as wide as in *M. rufiventris* and *M. dilutus pythonissa*).

Abdomen similar to that of *M. dilutus pythonissa*, but with slightly less distinct microsculpture; posterior margin of tergite VII with palisade fringe.

♂: unknown.

Comparative notes: *Medon augur* is most similar to *M. dilutus pythonissa*, which is most unlikely to occur in Corsica and from which it is distinguished by the smaller and less prominent eyes and by the slightly shorter and narrower, uniformly ferrugineous elytra. *Medon rufiventris* is smaller, usually has a more wedge-shaped head, larger eyes and relatively longer and wider elytra. In the paler *M. dilutus dilutus*, the puncturation of the head and pronotum is finer and the median lines of head and pronotum are usually not free of punctures.

Distribution and bionomics: The species is represented only by its holotype from Corsica; the locality is not specified.

3.15. *Medon brunneus* (Erichson, 1839) (Map 8)

Lithocharis brunnea Erichson, 1839 (ERICHSON 1839: 513f).

Lathrobium megacephalum Heer, 1839 (HEER 1839: 238).

Lithocharis monticola Hampe, 1867 (HAMPE 1867: 372).

Medon robustior Roubal, 1920 (ROUBAL 1920: 150).

Medon olympicus Scheerpeltz, 1963b (SCHEERPELTZ 1963b: 439ff).

Types examined: See ASSING (2004a).

Additional material examined (total: 1300 exs.; for additional material see ASSING (2004a)):

Sweden: Skåne: 2 exs., Skäralid, 4.V.1973 & 6.XII.1975, leg. Gillerfors (cGil); 3 exs., same locality 6.V.1977, leg. Gillerfors (cGil); 2 exs., same locality, 17.IX.1996, leg. Gillerfors (cGil); 1 ex., same locality, 31.V.1997, leg. Gillerfors (cGil); 3 exs., Hall. Väderö, 2.XI.1974, leg. Gillerfors (cGil); 1 ex., Hall. Väderö, 31.VIII.1985, leg. Gillerfors (cGil).

Spain: Cataluña: 1 ex., Gerona, Ripoll, 11.III.1978 (cAss); 3 exs., Ripoll – Vic, leg. Franz (NHMW); 1 ex., Gerona, 7 km S Vidreras, 41°43N, 02°50E, 150 m, oak forest, 10.X.1997, leg. Zerche (cAss); 5 exs., 40 km N Barcelona, Sierra de Montseny, S-slope, 700 m, 19.III.1994, leg. Assing (cAss); 1 ex., Sierra de Montseny, 1400 m, beech forest, 19.III.1994, leg. Wunderle (cWun); 1 ex., Sierra de Montseny (cBor); 1 ex., Sierra de Montseny, 1100 m, 20.IV.1999, leg. Tronquet (cTro); 1 ex., same data, but 1800 m (cTro).

England: 1 ex., Kent, Maidstone, 23.IV.1990, leg. Owen (cOwe).

France: Languedoc-Roussillon: 8 exs., N Nimes, Pont du Gard, leg. Franz (NHMW, cAss); 5 exs., Gard, W Nimes, Dions, 19.V.1994, leg. Schülke (cSch); 1 ex., Hérault, St. Jean de Buèges, 17.VI.2000, leg. Tronquet (cTro); 12 exs., Prats de Mollo, leg. Franz, Giraud (MHNG, NHMW, cAss); 1 ex., same locality, 26.V.1937, leg. Giraud (MHNG); 1 ex., Pyrénées Orientales, Argelès, Vallé de la Massane, leg. Franz (cAss); 1 ex., Molitg les Bains, 600 m, 13.VI.1995, leg.Tronquet (cTro); 1 ex., same data, but 28.V.1995 (cTro); 1 ex., Molitg les Bains, 700 m, 7.III.1999, leg.Tronquet (cTro); 1 ex., Campôme, 700 m, 16.XI.1996, leg. Tronquet (cTro); 1 ex., Campôme, 800 m, 24.VI.1995, leg. Tronquet (cTro); 2 exs., forêt de Boucheville near Rabouillet [42°45N, 2°21E], 750-650 m, 27.II.2001, leg. Tronquet (cTro). **Aquitaine:** 1 ex., Dordogne, Brantôme (MHNG); 1 ex., Dordogne, Le Bugue, 3.VIII.1941 (MHNG); 1 ex., Gironde, Sadirac, 22.IV.1939, leg. Tempère (MHNG); 3 exs., Léognan, 26.IV.1936, leg. Tempère (MHNG). **Bretagne:** 3 exs., Forêt de Huelgoat, leg. Franz (NHMW, cAss). **Normandie:** 1 ex., Caen (NHMW); 6 exs., Rouen (NHMW). **Île-de-France:** 1 ex., Paris [paralectotype of *Lithocharis picea* Kraatz]. **Bourgogne:** 1 ex., Nièvre, Brassy, leg. Mequignon (MHNG); 2 exs., Nièvre, Dun-les-Places, VII.1903, leg. Mequignon (MHNG). **Champagne-Ardenne:** 3 exs., Épernay (MHNG); 1 ex., Marne, Ft. de Troisfontaine (MHNG). **Centre:** 3 exs., Perrusson, leg. Mequignon (MHNG). **Provence:** 3 exs., Vaucluse, Plateau de Vaucluse, Gorge de Nesque, 500 m, 28.XII.1995, leg. Assing & Stüben (cAss); 3 exs., Vaucluse, Mt. Ventoux near Mt. Serein, 1000 m, 27.XII.1995, leg. Assing & Stüben (cAss); 1 ex., Vaucluse, Montagne du Luberon, Apt, S Auribean, 700 - 800 m, 29.XII.1995, leg. Assing & Stüben (cAss); 2 exs., Carpentras, Vénasque, 300 m, 5.VIII.1997, leg. Stüben (cAss); 4 exs., Tanneron, 350 m, 26.V.1991, leg. Wunderle (cWun); 1 ex., Tanneron, VI.1988, leg. Wunderle (cWun); 4 exs., Le Beausset, 30.VII.1921 (MHNG); 1 ex., Port-Cros, IV.1962 (MHNG); 1 ex., Ollioules, XI.1960 (MHNG); 1 ex., Lantosque (cBor); 3 exs., Sophia Antipolis near Antibes, haystack, 16.X.1991, leg. Schülke (cSch); 9 exs., Col de Castillion, N Monti, 350 m, 5.V.1996, leg. Wolf (cSch); 2 exs., road from Col de Castillion to Col de Braus, 700 m, 8.V.1996, leg. Wolf (cSch); 5 exs., Col de Braus, 1000 - 1150 m, 7.V.1996, leg. Wolf (cSch); 1 ex., SE Sospel, Albarée, 860 m, 9.V.1996, leg. Wolf (cSch); 10 exs., Menton, Annonciade, 13.XI.1983, leg. Zoia (cZan); 4 exs., Mandelieu, 6.XII.1992, leg. Zoia (cZan); 1 ex., St.-Vallier-de-Thiey, leg. Toumayeff (MHNG); 2 exs., same data, but VI.1968 (MHNG); 2 exs., same data, but VIII.1969 (MHNG); 1 ex., same data, but VIII.1976 (MHNG); 2 exs., same locality, leg. Sainte Claire Deville (MHNG); 1 ex., Nice, La Lanterne, XII.1956 (MHNG); 2 exs., Nice, 25.VIII.1921 (MHNG); 1 ex., Nice, leg. Bedel (MHNG); 2 exs., St. Augustin, III.1958 (MHNG); 1 ex., St. Augustin, leg. Ochs (MHNG); 1 ex., Beaulieu-sur-Mer, 1.IV.1932 (MHNG); 1 ex., Theoule (MHNG). **Rhône-Alpes:** 1 ex., Bourg-en-Bresse, 450 m, 10.VIII.1997, leg. Stüben (cAss); 1 ex., Voiron, 17.VII.1972 (cBor); 1 ex., Cevennes, Col de l´Escrinet, 790 m, 8.-9.VI.1999, leg. Wolf (cSch); 1 ex., W Tullins, road from Venrey to Grenoble, 300 m, 26.VI.1999, leg. Wolf (cSch); 1 ex., Gorges de l´Ardeche, near Grotte de la Madeleine, 10.VI.1999, leg. Wolf (cSch); 1 ex., Saint Jean d´Conz, 15 km W Chambery, C. la Bruyere, 650 m, 26.VI.1999, leg. Wolf (cSch); 1 ex., Ain, Cerdon, I.1948 (MHNG); 3 exs., Ain, La London [46°10N, 06°01E], 12.VII.1961, 7.IX.1964, leg. Comellini (MHNG); 3 exs., Ain, Longeray [46°06N, 05°53E], 15.XII.1961, leg. Comellini (MHNG); 7 exs., Savoie, Pont-du-Fier, 5.X.1960, leg. Comellini (MHNG); 1 ex., Savoie, forêt de St. Hugon, VII.19124 (MHNG); 1 ex., Savoie, St.-Alban, 15.IX.1960, leg. Comellini (MHNG); 1 ex., Haute-Savoie, Iles d´Arve [46°12N, 06°08E], 30.V.1959, leg. Comellini (MHNG); 2 exs., Haute-Savoie, Allinges, VII.1960, leg. Comellini (MHNG); 1 ex., Haute-Savoie, Dingy-en-Vuache, 12.II.1961, leg. Comellini (MHNG); 2 exs., Haute-Savoie, Vulbens, 9.V.1960 & 9.V.1961, leg. Comellini (MHNG); 3 exs., Haute-Savoie, Rumilly, 10.X.1959, leg. Comellini (MHNG); 1 ex., Haute-Savoie, Arcine, 1.V.1961, leg. Comellini (MHNG); 1 ex., Haute-Savoie, Chamonix, La Fégére (MHNG); 1 ex., Rhône, Vaugneray (MHNG); 3 exs., Drôme, Valence (MHNG). **Locality illegible:** 4 exs. (MHNG).

Monaco: 3 exs., Monaco (MHNG).

Switzerland: 1 ex., Bern, Gümmenen, 19.IV.1986, leg. Feller (cSch); 1 ex., Bern, Gallmitz, 7.IV.1986, leg. Feller (cSch); 4 ex., Vaud, Morges (NHMW).

Belgium: 1 ex., Spa, 6.IV.1983, leg. Assing (cAss).

Germany: Nordrhein-Westfalen: 8 exs., Porta Westfalica, Wittekindsberg, oak forest, 10.VI.1993, leg. Assing (cAss); 1 ex., Höxter, Beverungen, 17.V.1990, (cAss); 3 exs., Menden, Hönnetal, Klusenstein, XI.1994 & 29.IV.1996, leg. Feldmann (cFel); 1 ex., Rosbach, leg. Katschak (cFel); 1 ex., Nachrodt, 200 m, XII.1997, leg. Feldmann (cFel); 3 exs., Brühl near Köln, Staatsforst Ville, 2.VIII.1989, leg. Köhler (cKöh, cWun); 1 ex., same data, but 23.VII.1988 (cKöh); 1 ex., Radevormwald, 29.X.1985, leg. Wenzel (cKöh). **Rheinland-Pfalz:** 1 ex., Lahnstein, NSG "Koppelstein", 18.VIII.1985, leg. Wunderle (cWun); 1 ex., Altenahr, Vischeltal, 17.VIII.1985, leg. Wunderle (cWun); 1 ex., Altenahr, vineyard, 2.VI.1984, leg. Wunderle (cWun); 2 exs., Altenahr, Langfigtal, 11.IV.1987, leg. Köhler, Wunderle (cKöh, cWun); 1 ex., Altenahr, Reimertzhoven, 1.IV.1987, leg. Köhler (cKöh); 1 ex., Eifel, Gemünd, Kermeter, Am Steinbach, 23.VI.1992, el. Köhler (cKöh); 3 exs., 3 km S Ahrweiler, 18.IX.1980, leg. Scheuern (cWun). **Baden-Württemberg:** 1 ex., Wyhlen, 20.VIII.1978, leg. Kiener (MHNG). **Schleswig-Holstein:** 3 exs., Ratzeburg, 3.IV.1988, leg. Wunderle (cWun). **Niedersachsen:** 2 exs., Ith, Coppenbrügge, 29.IX.1991, leg. Assing (cAss); 1 ex., same data, 14.X.1984 (cAss); 2 exs., Ith, Lauenstein, 300 m, mixed forest, pitfall trap, 28.VII., 2.IX. & 6.XII.1990 (cAss); 1 ex., same locality, 6.VIII.1988 (cAss). **Hessen:** 2 exs., Marburg, Caldern, 5.V.1984, leg. Wunderle (cWun); 1 ex., Rasdorf (MHNG); 1 ex., Darmstadt (NHMW).

Bayern: 1 ex., Bad Feilnbach, IV.1999, leg. Feldmann (cFel); 4 exs., Chiemgau, Kampenwand, 1000 m, 4.VIII.1995, leg. Wolf (cSch); 2 exs., Königssee, 23.IX.1949, leg. Benick (MHNG). **Mecklenburg-Vorpommern:** 1 ex., Rügen, Lohme, 26.VII.1984, leg. Behne (cSch); 1 ex., S Lohme, 1.X.1989, leg. Zerche (DEI). **Sachsen-Anhalt:** 1 ex., LKr. Sangerhausen, Questenberg, 26.VI.1998, leg. Schülke (cSch). **Brandenburg/Berlin:** 3 exs., Pusack, deciduous forest, 25.IX.1999, leg. Wrase (cSch); 16 exs., Eberswalde, coll. Neresheimer (DEI). **Sachsen:** 3 exs., Meissen, Zadel, 3.IV.1976 (cSch); 2 exs., Dresden, NSG Rotstein near Sohland, 8.X.1988, leg. Zerche (DEI); 2 exs., Dresden, Zittauer Geb., NSG Lausche, 7.X.1988, leg. Zerche (DEI). **Locality not specified:** 1 ex. (MHNG).

Italy: Trentino-Alto Adige: 1 ex., Wals near Kaltern, 25.VII.1973 (cAss); 1 ex., Pieve di Ledro, 30.VIII.1972, leg. Pace (cBor); 2 exs., Bressanone (BZ), Tiles, 800-1000m, 30.VII.1973, leg. Sette (cZan); 4 exs., Tiles, VIII.1975, leg. Sette (cZan); 1 ex., Smarano (TN); VII.1972, leg. Zanetti (cZan); 1 ex., same locality, 1000m, 11.VII.1973 (cZan); 2 exs., same data, but 11.VII.1974 (cZan); 2 exs., same data, 21.VIII.1996 (cZan); 1 ex., Trento (NHMW). **Piemonte:** 1 ex., Abbazia, 23.XII.1934, leg. Springer (UCBA). **Lombardia:** 6 exs., Alpi Orobi, Morbegno, 350 m, deciduous forest, 10.VIII.1994, leg. Assing (cAss); 4 exs., Val Formazza, N Domodossola, 1050 m, 1.VIII.1996, leg. Wolf (cSch); 1 ex., Mantova, Bosco Fontana, 27.X.1980, leg. Zanetti (cZan). **Veneto:** 1 ex., Fongara, 21.V.1972, leg. Pace (cBor); 1 ex., Valli del Pasubio, 9.V.1972, leg. Pace (cBor); 1 ex., San Giovanni Ilarione, 7.V.1972, leg. Pace (cBor); 1 ex., Belluno, 23.IV.1973, leg. Garagnani (cBor); 2 exs., Feltre (BL), 1.V.1973 (cZan); 7 exs., Pieve d´Alpago (BL), 22.VII.1961 (UCBA, cZan); 1 ex., Valdagno (VI), 21.V.1972, leg. Zanetti (cZan). **Friuli-Venezia-Giulia:** 1 ex., Tagliamento near Comino, 46°13N, 13°01E, 50 m, 12.IX.1998, leg. Schülke (cSch); 2 exs., E Cividale del Friuli, Podresca, 750m, 30.V.1986, leg. Torti (cZan); 1 ex., E Trieste, Grópada, 3.IX.1980, leg. Seriani (Zan); 3 exs., Aurisina (TS), 29.V.1986, leg. Torti (cZan); 29 exs., Trieste env. (NHMW); 14 exs., Trieste, Opacina-Basovizza, V.-VI.1921, leg. Moczarski & Scheerpeltz (NHMW). **Emilia-Romana:** 1 ex., NW Imola, Mte. Calderano, 570 m, 9.V.1997, leg. Wolf (cSch). **Toscana:** 8 exs., 30 km SW Firenze, Figline Valdarno, 200 m, 14.VI.1992, leg. Assing (cAss); 1 ex., Monticiano, R. N. Alto Merse, 8.II.1999, leg. Meybohm (cAss); 1 ex., Mt. di Calvani (FI), Mungona, 650 m, 1.V.1991, leg. Wunderle (cWun); 3 exs., Siena Vecchia (SI), 300 m, 9.V.1991, leg. Wunderle (cWun); 1 ex., Mt. Falterona, Castagno di Andrea, 700 m, 7.V.1991, leg. Wunderle (cAss); 2 exs., Ruota, XI.1971, leg. Bordoni (cBor); 1 ex., N Borgo San Lorenzo, Grezzano, X.1971, leg. Bordoni (cBor); 2 exs., S Massa, Lago dell´Accesa, 3.X.1995, leg. Bordoni (cBor); 4 exs., P.so Viamaggio (AR), 830m, oak forest, 2.V.1986, leg. Zoia (cZan); 13 exs., Radicondoli (SI), 3.IV.1994 (cZan); 3 exs., Petriolo, 3.XI.1972, leg. Castellini (cTro); 5 exs., Cantagallo, IX.1976, leg. Castellini (cTro). **Umbria:** 2 exs., Lago di Trasimeno, Monte Solare, 400 m, 24.V.1998, leg. Wolf (cSch); 3 exs., Castiglione del Lago (PG), Pozzuolo, oak forest, 2.V.1986, leg. Zoia (cZan). **Abruzzi:** 15 exs., Torino di Sangro, 24.-26.VII.1974, leg. Pace (cBor). **Campania:** 2 exs., Napoli, Ischia, S. Angelo, 27.X.1936, leg. Benick (cAss); 5 exs., Napoli, Caserta, X.1924, leg. Andreini (cBor); 1 ex., Novi Velia, 7.VIII.1973, leg. Pace (cBor); 1 ex., Monti Albumi, Salerno, W San Rufo, Pso. di Sentinella, 900 m, 10.X.2000, leg. Wolf (cSch); 1 ex., Salerno, E Paestum, Capaccio, Mte. Soprano, 350 m, 13.X.2000, leg. Wolf (cSch); 2 exs., NE Salerno, Monte Stella, leg. Liebmann (MHNG). **Lazio:** 2 exs., Monte Circeo, N-Slope, 300 - 450 m, *Quercus ilex* forest, 27.XII.1994, leg. Assing (cAss); 2 ex., Monti Lepini near Carpineto, 27.VI.1973, leg. Pace (cBor); 8 exs. Monti Aurunci NE Formia, 3.VII.1975, leg. Pace (cBor); 1 ex., Lago di Vico (UT), 10.XI.1974, leg. Rossi (cZan); 1 ex., Lago di Bracciano, Monti Sabatini, Mte. Guerrano, 500 m, 7.V.1998, leg. Wolf (cSch); 1 ex., Lago di Bracciani, 3 km N Orido Romano, 5.V.1998, leg. Wolf (cSch); 1 ex., 19 km S Rieti, Cerdomare, 19.V.1998, leg. Wolf (cSch); 2 exs., Itri (LT), 320m, 30.IX.1982, leg. Zoia (cZan); 5 exs., Colli Albani, Monte Cavo, 7.XI.1980, leg. Zoia (cZan); 3 exs., Colli Albani, Rocca di Papa, Monte Cavo, 600 - 800 m, 9.V.1998, leg. Wolf (cSch). **Puglia:** 2 exs., Gargano, W San Marco in Lámis, Montenero, 900 m, oak forest, 30.XII.1994, leg. Assing (cAss); 4 exs., Gargano, 16.VIII.1974, leg. Pace (cBor); 1 ex., Foresta Umbra, Foggia, VII.1972, leg. Sciaky (UCBA); 1 ex., Foresta Umbra, 22.VI.1967, leg. Lohse (MHNG); 3 exs., B. Umbra, 26.V.1913, leg. Fiori (UCBA). **Basilicata:** 1 ex., Maratea, 40°01N, 15°44E, 485 m, 12.V.2002, leg. Wunderle (cWun); 1 ex., 12 km SSW Latrónico, 40°01N, 15°58W, 635 m, 9.V.2002, leg. Wunderle (cWun); 2 exs., Potenza, W San Mauro Forte, Accettura, 600 - 780 m, 22.X.2000, leg. Wolf (cSch). **Calabria:** 1 ex., Orsomarso (CS), 1.VII.1986, leg. Angelini (cZan); 4 exs., Orsomarso, Grisolia (CS), 700 m, 17.VI.1997, leg. Angelini (cZan).

Austria: Vorarlberg: 3 exs., Gebhardsberg (NHMW). **Oberösterreich:** 1 ex., Windischgarsten, leg. Franz (NHMW); 1 ex., Gmunden, leg. Franz (NHMW); 1 ex., Weyr, leg. Franz (NHMW); 1 ex., Kleinreifling, leg. Franz (NHMW). **Tirol:** 7 exs., Hall, 1200 m, 7.VIII.1997, leg. Wolf (cSch). **Salzburg:** 1 ex., Mandling, leg. Franz (NHMW). **Niederösterreich/Wien:** 2 exs., Frankenfels, leg. Franz (NHMW); 1 ex., Hardegg, leg. Franz (NHMW); 2 exs., Haslau, leg. Scheerpeltz (NHMW); 26 exs., Mödling, leg. Franz, Mandl, Scheerpeltz (NHMW); 1 ex., Tullnerbach, leg. Scheerpeltz (NHMW); 2 exs., Vöslau, leg. Franz (NHMW); 1 ex., Krenngraben near Kl. Hollenstein, leg. Franz (NHMW); 1 ex., Donauauen, Wolfsthal, leg. Franz (NHMW); 1 ex., Ebreichsdorf, mole nest, leg. Franz (NHMW); 3 exs., Wien (NHMW); 2 exs., Hütteldorf (NHMW); 1 ex., Neuwaldegg (NHMW); 2 exs., Wien, Weidlingau (NHMW); 2 exs., Rodaun (NHMW); 1 ex., Wien, Prater, leg. Franz (NHMW); 1 ex., Wienerwald, Hadersdorf, leg. Skalitzky (NHMW); 12 exs., Wienerwald, Rekawinkel, leg. Scheerpeltz, Skalitzky (NHMW); 2 exs., Wien, Bisamberg, leg. Skalitzky, Scheerpeltz (NHMW); 4 exs., Pressbaum, leg. Scheerepeltz (NHMW); 1 ex., Lunz (MHNG); 3 exs., Scheibbs, 24.VII.1970, leg. Resse (MHNG); 16 exs., 4 km SE Hof am Liethberge, Franz-Joseph-Warte, 47°56N, 16°37E, 480 m, deciduous forest, 15.X.1998, leg. Zerche (DEI); 2 exs., Brühl, leg. Schuster (NHMW); 6 exs., Leithagebirge (NHMW; 1 ex., Schneeberg (NHMW); 2 ex., Rabenstein (NHMW); Tullnerbach, leg. Scheerpeltz (NHMW). **Steiermark:** 7 exs., Mühlbachgraben near Rein, leg. Franz (NHMW); 1 ex., Pass im Stein, leg. Franz (NHMW); 2 exs., Peggau, leg. Franz (NHMW); 1 ex., Frauenstein, leg. Franz (NHMW); 1 ex., Tüffer, leg. Franz (NHMW); 1 ex., Ringkogel, Hartberg, leg. Franz (NHMW); 1 ex., Hochschwab, Bodenbauer, leg. Wimmer (NHMW); 1 ex., Tobelbad (MHNG); 13 exs., Pleschkogel near Rein, 470 m, 20.VI.1999, leg. Zerche (DEI). **Kärnten:** 1 ex., Flattach, Mölltal, leg. Franz (NHMW); 1 ex., Saualpe, Eberstein, 17.VII.1986, leg. Wunderle (cWun); 1 ex., Karnische Alpen, Weidenburger Wasserfall near Weidenburg, 17.-20.IX.1987, leg. Wunderle (cWun); 1 ex., Maria Rain (NHMW); 1 ex., Waidisch, leg. Mandl (NHMW); 1 ex., Dobratsch (NHMW); 1 ex., Gailtaler Alpen, Presseggen (NHMW). **Burgenland:** 1 ex., Rechnitz, leg. Franz (NHMW); 2 exs., Geschriebenstein, leg. Franz (NHMW); 4 exs., Eisenberg near Burg, leg. Franz (NHMW); 2 exs., Leithagebirge, Zeilerberg, 24.VIII.1983, leg. Assing (cAss); 17 exs., Leithagebirge, Purbach, leg. Franz (NHMW); 5 exs., Leithagebirge, Wimpassing, leg. Franz (NHMW); 1 ex., Leithagebirge, Winden, leg. Franz (NHMW); 1 ex., Donnerskirchen, leg. Franz (NHMW); 2 exs., Ruster Hügelzug, leg. Franz (NHMW); 1 ex., Rust, pasture, 11.VII.1973 (cAss); 43 exs., Zurndorf, leg. Franz (NHMW); 1 ex., Nickelsdorf, leg. Franz (NHMW); 1 ex., Neusiedlersee, eastern lakeshore, leg. Franz (NHMW); 1 ex., Groß-Petersdorf, leg. Franz (NHMW); 1 ex., Leithagebirge (MHNG); 20 exs., Neudorf (NHMW). **Locality ambiguous:** 4 exs., Gaming (MHNG).

Slovakia: 1 ex., Velka Fatra, Blatnica, 900 m, 11.VII.1992, leg. Assing (cAss); 1 ex., Nový Salas, Presev, 8.V.1998, leg. Smatana (cSch); 3 exs., Pezinok, 400m, 14.VIII.1992, leg. Zoia (cZan); 2 exs., Hrhov, 3.V.1967, leg. Lohse (MHNG); 2 exs., Mala Fatra, Rieka W Kralovany, Chata Sútovska dolina, 40°10N, 19°05E, 500 m, 24.VII.2001, leg. Zerche (DEI); 4 exs., E Bánovce, E Ostrý Vrach peak, 48°44N, 18°22E, 520 m, beech forest, 3.VIII.2001, leg. Zerche (DEI); 3 exs., Slovenský kras, W Bôrka, 48°38N, 20°47E, 655 m, beech forest, 29.VII.2001, leg. Zerche (DEI); 2 exs., Pieninsky naroden park, 18.VII.1993, leg. Zerche (DEI); 1 ex., Bratislava, Svaty jur, 220 m, 26.V.1991, leg. Behne (DEI); 2 exs., Pieniny Geb., Lesnica 500 m, 11.-14.VI.1990, leg. Behne (DEI); 3 exs., Nitra (NHMW); 3 exs., Herlany, 15.V.2000, leg. Hlavač (cAss).

Slovakian or Polish territory: 2 ex., "Beskiden" (NHMW).

Czech Republic: 5 exs., Prag env. (NHMW); 2 ex., "Erzgebirge, Hamergrund" (NHMW); 2 exs., "Hof" (NHMW); 1 ex., Oskau (NHMW).

Slovenia: 6 exs., Celje, leg. Franz (NHMW); 1 ex., Lipica, 27.VI.1981 (cAss); 1 ex., Mozelj Kocevje, 500 m, mixed forest, 11.V.1993, leg. Gasparo (cZan); 7 exs., Senožeče, 7.VIII.1969, leg. Besuchet (MHNG); 2 exs., Podčetrtek, 26.IV.1930, leg. Kodrik (MHNG); 2 exs. Postojna (NHMW); 5 exs., "Wochein" (NHMW).

Hungaria: 2 ex., Sopron (NHMW); 3 exs., Budapest (NHMW; 8 exs., locality not specified or not identified (NHMW).

Romania: 1 ex., Brasov (MHNG); 4 exs., Bihar (NHMW); 8 exs., Băile Herculane (NHMW); 2 exs., "Roterturm Pass" (NHMW); 1 ex., Sinaia (NHMW); 1 ex., Azuga (NHMW); 2 exs, Tismana (NHMW); 1 ex., Campu Selului (NHMW); 1 ex., Gaia Arama (NHMW)

Bulgaria: 4 exs., Pirin, leg. Weirather (MHNG).

Croatia: 1 ex., Ridnik-Karlovac, 30.IV.1990, leg. Wunderle (cWun); 1 ex., Istria, Opatija, Mt. Učka, 250 m, 24.VI.1996, leg. Wolf (cSch); 5 exs., same data, but 950 m (cSch); 5 exs., Pula, 13.IV.1974, leg. Zoia (UCBA); 6 exs., Pula (NHMW); 1 ex., Plitvice, 18.VIII.1977, leg. Lohse (MHNG); 1 ex., Plitvice (NHMW); 19 exs., Opatija (NHMW); 8 exs., Noghera (NHMW); 34 exs., Rab island (NHMW); 9 exs., Mljet island (NHMW); 16 exs., Velebit (NHMW); 3 exs., Radostak (NHMW).

Bosnia-Herzegovina: 1 ex., Prozor, 16.VIII.1977, leg. Lohse (MHNG); 4 exs., Bjelasnica, 15.VIII.1977, leg. Lohse (MHNG); 5 exs., Bjelasnica (MHNG); 5 exs., Nevesinje (NHMW); 4 exs., Jablanica (NHMW); 2 exs., Metkovic (NHMW); 3 exs., Majevica planina (NHMW); 5 exs., Travnik, 30.V.1934, leg. Natterer (NHMW); 3 ex., Čelič (NHMW); 4 exs., Žepče (NHMW); 5 exs., Sarajevo (NHMW).

Serbia-Montenegro: 1 ex., Lovcen (NHMW); 6 exs., Bojana range (NHMW); 18 exs., Rtanj Planina, leg.

Breit (NHMW); 2 exs., Visočka Ržana, Pirot, 750 m, 29.IV.2002, leg. Hlavač (cAss).

Macedonia: 1 ex., Koševo, leg. Pfeiffer (MHNG); 5 exs., northern shore of lake Prespa, 23.IX.1958, leg. Schuster (NHMW); 3 exs., Monastir (NHMW).

Albania: 5 exs., Krujë, leg. Mader (NHMW); 2 exs., Sarisaltik, 1180m, leg. Mader (NHMW).

Greece: 6 exs., Pindos, Kalivia, 28.-29.V.1989, leg. Zoia (cZan); 4 exs., Evvoia, Pagóndas, 4.IV.1983, leg. Zoia (cZan); 2 exs., Evvoia, Dirfys, 1.III.1983, leg. Zoia (cZan); 1 ex., Pelopónnisos, Olympia, O. Alfios, 7.IX.1995, leg. Zoia (cZan); 38 exs., Pilion (NHMW); 22 exs., Parnassos Oros (NHMW); 6 exs., Athina (NHMW); 1 ex., Sfendali (NHMW); 12 exs., Nisista, Xeravunei (NHMW); 2 exs., Pelopónnisos, Patras, 22.III.1971, leg. Löbl (MHNG); 4 exs., Pelopónnisos, Kalavrita, 800 m, 3.IV.1971, leg. Löbl (MHNG); 1 ex., Pelopónnisos, Enochorion (NHMW); 1 ex., Pelopónnisos, Olympia, Ladzoi, 100 m, 22.III.1992, leg. Frisch (MNHUB); 1 ex., Pelopónnisos, Taygetos, Kalamata-Sparta, 1300 m, 1.IV.1992, leg. Frisch (MNHUB):.1 ex., Taygetos (NHMW); 6 exs., Drama, Falakró, leg. Weirather (MHNG, cBor); 1 ex., Zakynthos, Skopos, 24.III.1971, leg. Löbl (cBor); 6 exs., Kefallinia, Sami, 31.III.&2.IV.1971, leg. Löbl (MHNG); 1 ex., Kefallinia, Oros Aenos, 31.III.1971, leg. Mahnert (MHNG); 13 exs., Kefallinia, several collectors (NHMW); 12 exs., Lefkas, Moni near Fryni, 27.III.1971, leg. Hauser (MHNG); 44 exs., Lefkas, several collectors (NHMW); 1 ex., Zante, 1809, leg. Hilf (NHMW); 50 exs., Corfu, leg. Beier, Hummler, Moczarski (MHNG, NHMW); 2 ex., Crete, Amari, leg. Biró (NHMW).

Ukraine: 1 ex., Crimea, Evpatoria, 10.-20.VII.1999 (cSch).

Turkey: 22 exs., Kırklareli, Demirköy, 31.VII.1969, leg. Besuchet (MHNG, cAss); 4 exs., Istanbul, "Forêt de Belgrade", 4.VI.1967, leg. Besuchet (MHNG); 1 ex., same data, but 10.VII.1969 (MHNG); 4 exs., Istanbul, Şile, 28.V.1967, leg. Besuchet (MHNG, cAss).

Locality not specified: 11 exs. (MHNG).

Diagnosis: See ASSING (2004a) and the key in Section 4.

Distribution and bionomics: *Medon brunneus* is a widespread Adriato-Mediterranean element (Map 8). Its distribution ranges from northwestern Turkey, southern Greece (including Crete), and southern Italy in the southeast and south, to southern Sweden and southern England in the north, and to western France and northeastern Spain in the west (material examined; ASSING 2004a). For additional records see e.g. BOHÁČ (1985), BRUGE et al. (2001), DRUGMAND (1989), FOWLER (1888), HANSEN (1996), HANSEN et al. (1995), HANSEN (1964), HORION (1965), HUGENTHOBLER (1966), KOCH (1968), KÖHLER & KLAUSNITZER (1998), LINKE (1907, 1913), LUNDBERG (1995), SCHILLER (1989), TERLUTTER (1995), and TRONQUET (2001). In Scandinavia, the species is present only in Denmark and southwestern Sweden: Skåne, Halland, Västergötland, Bohuslän (HANSEN 1964; LUNDBERG 1995). It is unknown from Norway, Finland, and the Baltic countries (SILFVERBERG 1992). HORION (1965) reports the species from Poland (two localities), Kiev (Ukraine), and from Russia (Wolyns´ka Oblast). The records from the Caucasus region must be considered doubtful until they are confirmed (ASSING 2004a). The species is very common in the southeast of its range: in the Balkans, Italy, and the southeast of Central Europe; it is much rarer in the northwest. In Italy, it is absent from Sicily and probably also from Sardinia. The records from the latter island (LUIGIONI 1929) are apparently based on misidentifications; I have seen no specimens from there. The previous record from the island of Pantelleria (CICERONI & ZANETTI 1995) refers to *M. despectus* (see Section 3.18). OUTERELO (1980) reports *M. brunneus* from Andalucía, stating that the species occurs in the whole Iberian Peninsula. These records are most likely to be based on misidentifications (confusion with *M. cauchoisi*). The occurrence of *M. brunneus* in the Iberian Peninsula is confined to the very northeast of Spain.

DRUGMAND (1989) states that the species is bivoltine, but there is no evidence supporting this. Based on the material examined here, *M. brunneus* is univoltine. According to HORION (1965), the species may be associated with nests of voles and/or mice, but there is still no striking evidence proving this. Previous records from mole nests are probably accidental; NOWOSAD (1990) found the species in only 7 nests out of 5000 nests studied. It is usually – and often in large numbers – found in the leaf litter of forests, especially deciduous forests (oak).

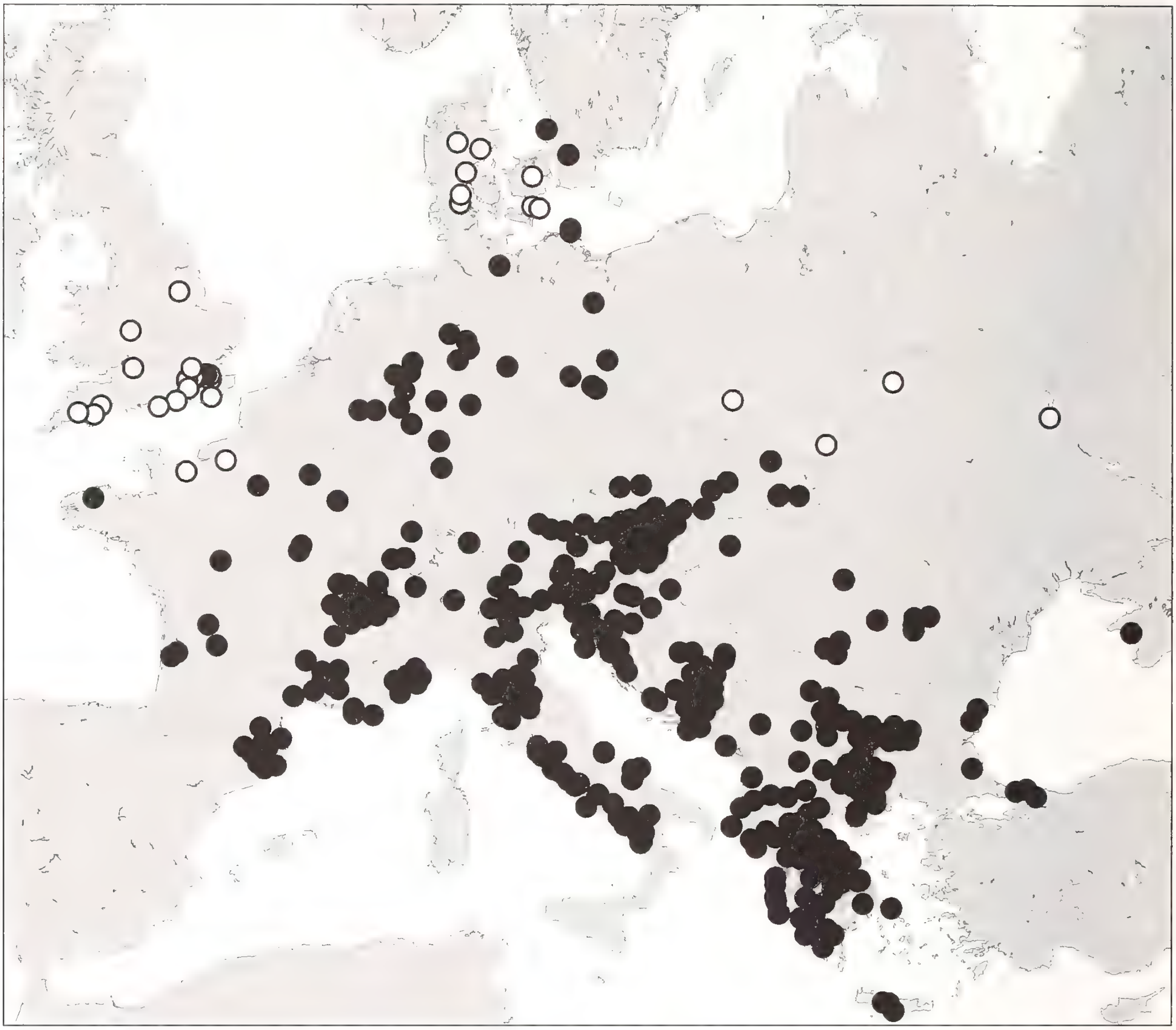
3.16. *Medon piceus* (Kraatz, 1858) (Figs. 74-78, Map 9)

Lithocharis picea Kraatz, 1858 (KRAATZ 1858: cxci f).

Medon muscicola Mulsant & Rey, 1878 (MULSANT & REY 1878: 128).

Medon murciensis Coiffait, 1970a (COIFFAIT 1970a: 715f) **syn. n.**

Types examined: *L. picea*: Lectotype ♂ [remounted, aedeagus dissected], here designated: Paris / Coll. Kraatz / Syntypus / Coll. DEI Eberswalde / Medon piceus (Kr.) V.I.Gusarov det. 1996 / Lectotypus ♂ *Lithocharis picea* Kraatz desig. V. Assing 2003 / Medon piceus (Kraatz) det. V. Assing 2003 (DEI). Paralectotypes: 1♂, 1♀: same data as lectotype (DEI); 1♂: same data, but "Medon brunneus (Erichson) det. V. Assing 2003" (DEI).



Map 8: Distribution of *Medon brunneus* (Erichson) (filled circles: revised records; open circles: selected literature records).

M. murciensis: Holotype ♂: Sierra de Espuña bei Murcia, Hi. m., lg. H. Franz / MUSEUM PARIS COLL H. COIFFAIT / HOLOTYPE / Medon burdigalensis Coiff. H. COIFFAIT det. 1969 / Medon piceus (Kraatz) det. V. Assing 2003 (MNHNP).

Comments: One of the syntypes of *Lithocharis picea* is conspecific with *M. brunneus* (Erichson), the others are in agreement with the long-standing interpretation of the species. Since the type series is a mixture of two species, a lectotype designation is mandatory, in order to unambiguously define the name; the male in better condition was selected as the lectotype.

In the original description of *M. murciensis*, which is based on a single male, COIFFAIT (1970a) compares the species with *M. ripicola* (Kraatz). An examination of the holotype revealed, however, that it is conspecific with *M. piceus* (Kraatz), so that the junior name *M. murciensis* is here placed in the synonymy of that species.

Additional material examined (total: 677 exs.)**:**

Portugal: 2 exs., Serra do Geres, Portela de Homem, 41°48N, 08°08W, 750 m, oak forest, 23.III.2002, leg. Lompe (cAss); 5 exs., Serra do Geres, Puerto la d´Home, leg. Franz (NHMW); 2 exs., Serra do Geres, 800 m, oak forest, 16.V.1992, leg. Wunderle (cWun); 1 ex., Serra de Montezinho, Rio Sabor, 41°54N, 06°47W, 900 m, poplar litter, 21.III.2002, leg. Meybohm (cAss); 1 ex., Serra de Estrela, S Manteigas, 40°22N, 07°33W, 980 m, oak forest, 18.III.2002, leg. Lompe (cAss); 2 exs., Serra da Estrela, S Manteigas, 40°21N, 07°34W, 1070 m, 19.III.2002, leg. Lompe (cAss); 1 ex., Serra da Estrela, N Manteigas, 40°24N, 07°32W, 850 m, 19.III.2002, leg. Meybohm (cAss); 8 exs., Manteigas, 1000 - 1100 m, leg. Franz (NHMW); 10 exs., Serra da Estrela, leg. Franz (NHMW); 1 ex., Guarda, S Gouveia, 1100 m, 17.IV.1960, leg. Besuchet (cAss); 4 exs., Coimbra, leg. Paulino (NHMW); 1 ex., Coimbra (NHMW); 2 exs., Lisboa, Serra do Sintra, 24.V.1992, leg. Wunderle (cAss); 10 exs., Sintra, Lagoa Azul, 6.VI.1966, leg. Besuchet, Comellini (MHNG); 2 exs., Luso, V.1959, leg. Fagel (IRSNB); 41 exs., Algarve, 10 km N S. Brás de Alportel, 400 m, 4.VI.1992, leg. Wunderle (cWun, cAss, cSch); 22 exs., Algarve, Caldas de Monchique, V.-VI.1960, leg. Fagel (IRSNB); 1 ex., Algarve, Serra Monchique, E Monchique, 37°19N, 8°31W, 530 m, 10.IV.2002, leg. Meybohm (cAss).

Spain: País Vasco: 2 exs., Sierra de Cantabria, ca. 30 km NW Logroño, NE Pipaón, 42°37´45N, 02°36´18W, 770m, oak forest with dense undergrowth, 14.X.2003, leg. Assing (cAss); 14 exs., Guizpúzcoa, pass between Elgoibar and Azcoitia, leg. Franz (NHMW). **Cantábria:** 2 exs., Santander, Monte de Candino, Liendo, leg. Franz (NHMW); 10 exs., Santander, Monte Aa, Ruente, leg. Franz (NHMW); 4 exs., Santander, Jesus de Montes, W Beranga, leg. Franz (NHMW); 2 exs., Santander, Marron, leg. Franz (NHMW); 1 ex., Santander, Puente Viesgo, leg. Franz (NHMW); 1 ex., Santander, Villaverde de Pontones, leg. Franz (NHMW); 5 exs., Pechon, Unquera, leg. Franz (NHMW); 1 ex., Reinosa, road to Alto de Campoo, 1400 m, 4.VI.1991, leg. Wunderle (cWun); 1 ex., Alto Campóo, 1600 m, oak forest, 4.VI.1991, leg. Zerche (DEI); 7 exs., same data, but 1400 m (DEI); 1 ex., Espinama, Puerto de Aliva, 28.VII.1972 (cBor); 2 exs., Picos de Europa, 10 km NNW Potes, 43°14´12N, 04°39´11W, 1025 m, N-slope, montane pasture, sifted from grass and moss, 17.VII.2003, leg. Assing (cAss). **Navarra:** 5 exs., Otxondo, 16.VII.1968, leg. Besuchet, Comellini (MHNG). **La Rioja:** 13 exs., Logroño, Monasterio de Valvamera, leg. Franz (NHMW). **Asturias:** 8 exs., Cabo Vidio, leg. Franz (NHMW); 8 exs., Posada, leg. Franz (NHMW); 2 exs., S Villaviciosa, leg. Franz (NHMW); 2 exs., Covadonga, leg. Franz (NHMW); 1 ex., Nueva, leg. Franz (NHMW); 8 exs., Arriondas, El Fito, VI.1965, leg. Fagel (IRSNB). **Galicia:** 3 exs., Lugo, Alto de Acebo-Cecos, 700 m, 31.VII.1992, leg. Tronquet (cTro); 3 exs., Lugo, Cruzul, Becerreá, leg. Franz (NHMW); 6 exs., Lugo, Valle de Lozera, leg. Franz (NHMW); 3 exs., Lugo, Villasouto, 2.X.2000, leg. Valcárcel (cSch, cAss); 1 ex., Lugo, Serra do Courel, Rio de Rofíón, 23.V.2000, leg. Valcárcel (cSch); 6 exs., Lugo, Monforte de Lemon, Gullade, 5.IX.2000, leg.. Valcárcel (cSch, cAss); 4 exs., Lugo, Sierra de Ancares, 2 km NE Doiras, 42°47N, 06°58W, 11.VI.2000, leg. Wrase (cSch); 4 exs., Sierra de Barbanza, Noia, leg. Franz (NHMW); 2 exs., Noia, leg. Franz (NHMW); 3 exs., Noia, Outes, leg. Franz (IRSNB, NHMW); 2 exs., La Coruña, San Saturnino, leg. Franz (NHMW); 1 ex., La Coruña, Punta de la Estaca, leg. Franz (NHMW); 1 ex., La Coruña, Puenteseco, leg. Franz (NHMW); 1 ex., Orense, Verin, Montes del Invernadero, Campo de Becerros, leg. Franz (NHMW); 6 exs., Santiago, Bosque de Cernadas, leg. Franz (NHMW); 2 exs., Santiago, Orilla del Rio Tambre, leg. Franz (NHMW); 10 exs., Prov. Pontevedra, Pontevedra, leg. Franz (NHMW); 4 exs., Pontevedra, Isla Cies del Norte, leg. Franz (NHMW); 1 ex., Pontevedra, Testeiro, 800 - 900 m, leg. Franz (NHMW); 2 exs., Pontevedra, Cabo Silieiro, Baiona, leg. Franz (NHMW); 2 exs., Pontevedra, A Lamosa, Sierra de Fonteiria, leg. Franz (NHMW); 2 exs., Pontevedra, leg. Franz (NHMW); 1 ex., Prov. Pontevedra, Rio Umia near Morana, leg. Franz (NHMW). **Castilla-León:** 3 exs., Sierra de la Demanda, ca. 40 km E Burgos, NE Valmala, Rábanos, 42°18N, 03°16W, 1190m, oak forest with grass, 12.X.2003, leg. Assing (cAss); 1 ex., Zamora, Lago de Sanabria, leg.Franz (NHMW); 11 exs., Ponferrada, leg. Paganetti (DEI, NHMW); 1 ex., Puerto de Bejar, 800-1400 m, V.-VI.1957, leg. Fagel (IRSNB). **Estremadura:** 1 ex., Prov. Badajoz, Puerto de las Marismas, 8.IV.1959, leg. Besuchet (MHNG). **Castilla-La Mancha:** 11 exs., SW Albacete, Sierra de Alcaraz, 15 km NNE Riópar, 38°32N, 02°25W, 1350 m, 7.IV.2003, leg. Assing (cAss); 9 exs., same data, but 38°35N, 02°21W, 1125 m, 10.IV.2003, leg. Assing (cAss); 1 ex., same data, but 38°34N, 02°20W, 1120 m, 10.IV.2003 (cAss); 1 ex., Albacete, leg. Comellini (MHNG). **Murcia:** 5 exs., Sierra de España, leg. Franz (NHMW); 2 exs., Sierra de Espuna, 26.III.1959, leg. Besuchet (MHNG). **Andalucía:** 1 ex., Sierra de Segura, Villaverde de Guadalimar, leg. Franz (NHMW); 1 ex., Jaén, Sierra de Segura, Embalse del Tranco, 38°10N, 2°48W, 15.VI.2001, leg. Starke (cFel); 2 exs., Jaén, Sierra de Cazorla, leg. Franz (NHMW); 3 exs., Sierra de Cazorla, Cazorla, source of Gualaquivir, 6.X.1993, leg. Wunderle (cWun); 15 exs., Sierra de Cazorla, 12.IV.1959, leg. Besuchet (MHNG); 6 exs., SE Ronda (MA), Sierra de Palmitera, 900 m, 24.III.1994, leg. Assing, Wunderle (cAss, cWun); 20 exs., Sierra de Bermeja (CA), Jubrique, 350 m, 26.III.1994, leg. Assing, Wunderle (cAss, cWun); 1 ex., Sierra de Bermeja, 1000 m, 26.III.1994, leg. Assing (cAss); 11 exs., Algeciras (CA), Sierra de Luna, 200 - 350 m, 28.III.1994, leg. Assing, Wunderle (cAss, cWun); 16 exs., Sierra de Luna, 27.V.1966, leg. Besuchet, Comellini (MHNG); 3 exs., Algeciras (CA), Sierra de Fates, 350 m, 28.III.1994, leg. Assing, Wunderle (cAss, cWun); 1 ex., Sierra Nevada, Pampaneira, 1000 m, 2.VIII.1991, leg.Sprick (cAss); 4 exs., Sierra Nevada, Lanjaron, 600 m, 23.III.1994, leg. Assing, Wunderle (cAss, cWun); 15 exs., Lanjaron, 26.IV.-18.V.1961, leg. Fagel (IRSNB); 1 ex., Sierra Nevada, leg. Franz (NHMW); 3 exs., Sierra Nevada, Guejar Sierra, 1200 m, 28.IX.1993, leg. Wunderle (cWun); 1 ex., Granada, Sierra de Baza, 37°20N, 02°54W, 1700 m, 14.IV.2001, leg. Sprick (cAss); 1 ex., Sierra de Córdoba, 9.IV.1959, leg. Besuchet (cBor); 1 ex., Algeciras, Sierra del Niño, 180m, 26.III.1987, leg. Zoia (cZan); 2 exs., Granada, Sierra de la Sagra, 1250 m, 21.V.1966, leg. Besuchet (MHNG); 1 ex., Cordoba, Villaviciosa, 29.VI.1969, leg. Comellini (MHNG); 12 exs., Huelva, Zalamea La Real, 6.VII.1969, leg. Comellini (MHNG); 4 exs., Cadiz, 10 km W Los Barrios, 36°11N, 05°34W, 210 m, sifted under cork trees, 10.II.1999, leg. Zerche (DEI); 1 ex., ca. 25 km N Almuñécar, Sierra de Almijara, 36°53N, 03°42W, ca. 1200 m, mixed pine, oak, and corktree forest, 25.XII.2003, leg. Assing (cAss).

England: 1 ex., Surrey, Leatherhead, Bookham Common, 24.V.1999, leg. Owen (cOwe).

France: Picardie: 1 ex., Pontarmé, 11.V.1969, leg. Tronquet (cBor). **Aquitaine:** 1 ex., Lot-et-Garonne, leg. Pandellé (NHMW); 1 ex., Bordeaux, 11.V.1952, leg. Tempère (MHNG); 1 ex., Gironde, Cazaux, 29.V.1904 (MHNG); 1 ex., Gironde, Facture, 6.VII.1929, leg. Tempère (MHNG); 1 ex., Gironde, locality illegible, 28.VIII.1931, leg. Tempère (MHNG); 1 ex., Gironde, Guzmet, 3.III.1928, leg. Tempère (MHNG); 1 ex., Gironde, Taussat-les-Bains, IV.1934, leg. Tempère (MHNG); 1 ex., Pyrénées Atlantiques, Sare, 400 m, 23.V.1966, leg. Tempère (MHNG); 2 exs., Sos, leg. Fauvel (DEI); 2 exs., Sos (NHMW). **Bretagne:** 7 exs., Morlaix, leg. Hervé (NHMW); 2 exs., Morlaix (NHMW). **Midi-Pyrénées:** 1 ex., Sarrant, 28.V.1936, leg. Giraud (MHNG); 5 exs., Hautes-Pyrénées, SW Bagnères-de-Luchon, Lac d´Oo, 1800 m, VII.1919 (NHMW); 5 exs., Saint-Sauveur-les-Bains near Luz-Saint-Sauveur, 17.IX.1965, leg. Tempère (MHNG). **Limousin:** 1 ex., Haute Vienne (NHMW). **Île-de-France:** 1 ex., Fontainebleau, 16.X.1938, leg. Moingeon (MHNG); 2 exs., Fontainebleau (MHNG); 1 ex., Versailles (MHNG); 1 ex., Paris (NHMW). **Auvergne:** 1 ex., Vichy, 12.VII.1934 (UCBA); 1 ex., Broût-Vernet, ant nest, 21.XII.1883 (MHNG). **Centre:** 2 exs., Bourges, leg. Boitel (MHNG); 4 exs., F. de Loches, leg. Mequignon (MHNG); 1 ex., Fréteval, leg. Mequignon (MHNG); 1 ex., Vendôme (MHNG); 1 ex., Perusson, leg. Mequignon (MHNG). **Rhône-Alpes:** 2 exs., Rhône, Charbonnières (MHNG); 1 ex., Ardèche, Vals-Les-Bains (MHNG). **Alsace:** 1 ex., Strasbourg, VII.1955 (MHNG). **Locality not identified or amgiguous:** 1 ex., Forêt de Moladier All., 23.X.1906 (cSch); 1 ex., St. Germain (MHNG); 1 ex., Las, leg. Fauvel (MHNG).

Netherlands: 1 ex., Nuenen, mole nest, 10.I.1976, leg. Kanaar (cSch).

Germany: Nordrhein-Westfalen: 13 exs., Kreis Steinfurt, Emsdettener Venn, 6.III.1999, leg. Assing, Wunderle (cAss, cWun); 3 exs., Kreis Steinfurt, N Hopsten, Wiechholz, 6.III.1999, leg. Assing, Wunderle (cAss, cWun); 1 ex., Neuss, 5.I.1978, leg. Koch (cAss); 1 ex., Vreden, Wallburg, 26.X.1992, leg. Terlutter (cFel); 1 ex., Vreden, Vredener Feld, 3.III.1993, leg. Terlutter (cFel); 3 exs., Troisdorf, Wahner Heide, 12.IV.1987, leg. Wunderle (cWun); 1 ex., Köln, Troisdorf, Wahner Heide, 21.III.1987, leg. Köhler (cKöh); 3 exs., Viersen, Ritzeroder Moor, 19.V.1990, leg. Wunderle (cWun); 2 exs., Brühl, Staatsforst Ville, 20.III.1987, 5.XI.1989, leg. Köhler (cKöh); 1 ex., Köln-Worringen, Worringer Bruch, 5.VIII.1996, leg. Köhler (cKöh); 2 exs., Kölner Bucht, Pulheim-Sinnersdorf, 14.III & 19.VI.1986 (cKöh); 2 exs., Kölner Bucht, Pulheim-Sinnersdorf, Chorbusch, 10.II.&2.VI.1986, leg. Köhler (cKöh); 1 ex., Mönchengladbach, Gerkerather Wald, 14.II.1986, leg. Köhler (cKöh); 1 ex., Münster-Wölbeck, Tiergarten, 5.VIII.1991, leg. Köhler (cKöh); 4 exs., Elmpt, Elmpter Bruch, 20.XI.1991, leg. Wunderle (cWun); 1 ex., Niederkrüchten, Elmpter Bruch, 20.XI.1991, leg. Köhler (cKöh). **Rheinland-Pfalz:** 3 exs., Lahnstein, NSG Koppelstein, 26.VI.1984 & 4.XI.1985, leg. Wunderle (cWun); 1 ex., Mainz (DEI); 1 ex., Wachenheim, Kammertsberg, 25.IV.1995, leg. Köhler (cKöh); 1 ex., Altenahr, Reimertzhoven, 11.IV.1987, leg. Köhler (cKöh); 1 ex., Ahrweiler (NHMW). **Schleswig-Holstein:** 1 ex., Schleswig, leg. Varendorff (NHMW). **Niedersachsen:** 1 ex., Lüneburger Heide, Niederhaverbeck, heathland, 15.XI.1993 (cAss); 1 ex., Lüneburg, Dahlenburg-Dahlem, 20.-21.VI.1994, leg. Köhler (cKöh); 3 exs., Soltau, Schneverdingen, 16.V.1998, 15.V.1999, 17.X.2000 (cAss); 1 ex., Winsen/Luhe, Laßrönne, 24.II.1995, leg. Assing (cAss); 76 exs., NW Hannover, Helstorf, heathland, 1980 - 1990 (cAss); 2 exs., Celle, Scheuen, heathland, XII.1984 (cAss); 1 ex., N Gifhorn, NSG “Heiliger Hain”, heathland, IX.1985 (cAss); 1 ex., Lehrte, Immensen, mixed forest, 30.IV.1986 (cAss); 1 ex., Meppen, Sprakeler Heide, heathland, IX.1987 (cAss); 2 exs., Oldenburg, Dötlingen, 22.IX.1970, leg. Lohse (MHNG); 1 ex., Oldenburg, Ostrittrum, 1.V.1971, leg. Lohse (MHNG). **Hessen:** 1 ex., Darmstadt, Eberstadt, beech forest, XI.1996, leg. Hetzel (cFel); 1 ex., Darmstadt, 15.VII.1958, leg. Vogt (cBor); 1 ex., Hanau (MHNG). **Baden-Württemberg:** 1 ex., Karlsruhe, Baden, 18.IV.1951, leg. Nowotny (MHNG). **Berlin/Brandenburg:** 1 ex., Schlaubetal, 9.I.1999, leg. Pütz (cAss); 1 ex., Berlin Karlshorst, Biesenhorster Sand, 9.IV.2001, leg. Nickel (cSch); 2 exs., NSG Rietzer See, 52°23N, 12°40E, pine forest, 11.V.1978, leg. Uhlig (DEI). **Thüringen:** 2 exs., Eisenberg (NHMW); 2 exs., locality not specified (DEI, NHMW).

Italy: 1 ex., Trentino-Alto Adige, Laces, 900 m, 10.V.1992, leg. Kapp (cKap).

Locality not specified: 5 exs. (MHNG).

Diagnosis: Highly variable species. 3.8-4.8 mm. Coloration somewhat variable; usual coloration: head black, pronotum dark brown to blackish brown, usually noticeably lighter than head; elytra brown to dark brown, usually slightly lighter than pronotum; abdomen dark brown to blackish brown with the apex, the lateral and often also the anterior margins of the segments lighter; legs and antennae reddish brown to ferrugineous, middle antennomeres often slightly darker than the basal and the apical ones.

Head of very variable shape, slightly oblong and approximately as wide as pronotum to weakly transverse and distinctly (ca. 1.15 x) wider than pronotum; eyes approximately half the length of postocular region or slightly larger; puncturation very variable, ranging from extremely dense and and fine, rendering the surface of the head almost completely matt, to moderately dense and coarser, with a small median area free of punctures, and with the interstices shining; punctures non-areolate; interstices with or without microsculpture (Figs. 74-75).

Pronotum, too, with puncturation of variable size and density; interstices without microsculpture; surface on the whole with more shine than that of head (Figs. 74-75)

Elytra of very variable size, 1.15-1.30 times as wide and at suture 1.05-1.17 times as long as pronotum (Fig. 74).

♂: protarsomeres I - IV not dilated; posterior margin of sternite VII shallowly concave and laterally with combs of usually 5-9 palisade setae (Fig. 76); sternite VIII not distinctive. Aedeagus with long and slender ventral process, its lateral margins subparallel, shape of apex (ventral view) somewhat variable, truncate to weakly convex, middle area of ventral process in cross-section concave (Figs. 77-78).

Comparative notes: Among its Western Palaearctic congeners, *M. piceus* is especially characterized by the shape of the aedeagus. In addition, it is distinguished by the following character combination: male protarsi not dilated, relatively dark coloration, puncturation of head dense, well defined, and not conspicuously coarse. In the collections examined, *M. piceus* was most often confused with *M. brunneus*, from which it is separated by its darker average coloration, the distinctly finer puncturation of the head, the longer and broader elytra, and by the shape of the aedeagus.

Distribution and bionomics: *Medon piceus* is an Atlanto-Mediterranean element (Map 9), its distribution ranging from the south of the Iberian Peninsula to the south of England and Central Europe (material examined). For a selection of additional records see BOHÁČ (1985), BRUGE et al. (2001), DRUGMAND (1989), FOWLER (1888), KOCH (1968), KÖHLER (2000), KÖHLER & KLAUSNITZER (1998), SCHILLER (1989), TERLUTTER (1995), and VOGEL (1979). *Medon piceus* is unknown from Scandinavia and the Baltic countries (HANSEN 1996; LUNDBERG 1995; SILFVERBERG 1992), and from southeastern Europe (ASSING 2004a). In the British Isles, it has been reported only from a few localities in southern England. According to LOTT & DUFF (2003), the species was last recorded from England in 1968, but OWEN (2000) indicates a recent record from Bookham. Apparently, the abundance of the species has increased in some areas of Central Europe since the beginning of the 20th century (HORION 1965), and there may have been a recent expansion at the northeastern limit of its range. The first record from the Czech Republic was by BOHÁČ (1981); only four years later the same author reported it from seven additional Czech localities (BOHÁČ 1985). The species is still unknown from Slovakia. Based on a written statement by Scheerpeltz, HORION (1965) maintains that, in Austria, *M. piceus* is "aus allen Bundesländern bekannt ...; zahlr. Belege in coll. Scheerpeltz"; however, the Scheerpeltz collection was examined and not a single Austrian specimen was found in this or in any other collection housed in the NHMW. Until the presence of *M. piceus* in Austria is confirmed, it should be deleted from the lists of Austrian Staphylinidae. Similarly, the species has been reported from various regions in Italy, including Sicily (CICERONI & ZANETTI 1995; LUIGIONI 1929; PORTA 1926; ROTTENBERG 1870), but I have seen only a single Italian specimen from the north (see material examined); KAHLEN (1987) reports the species from the same locality (Latsch = Laces). Most, if not all the other Italian records, however, are presumably based on misidentifications, as is suggested both by the revision of the material from various collections and the general distribution pattern of the species (Map 9). The record from Rhodos by SCHEERPELTZ (1964) is far outside the range of the species and doubtlessly erroneous. In the Iberian Peninsula, *M. piceus* is common in the south, the west and the northwest, but it is apparently absent from the northeast, where *M. cauchoisi* is abundant. Evidently, the species is much more common in the southwest than in the northeast of its range.

Medon piceus has been collected from various kinds of nests (moles, ants, etc.) (material examined; see also HORION (1965), RENNER & GRUNDMANN (1984)), but these observations are probably accidental. In Germany, the species is usually found in the leaf litter and humus of bogs, swamps, heathlands, and forests (mostly coniferous woods) with low-pH soils (material examined; HORION 1965; KOCH 1968; RENNER & GRUNDMANN 1984). In the Iberian Peninsula, according to personal observations, it occurs in various types of woodland (*Quercus ilex* and other oak species, pine forests, etc.) and in shrub habitats.

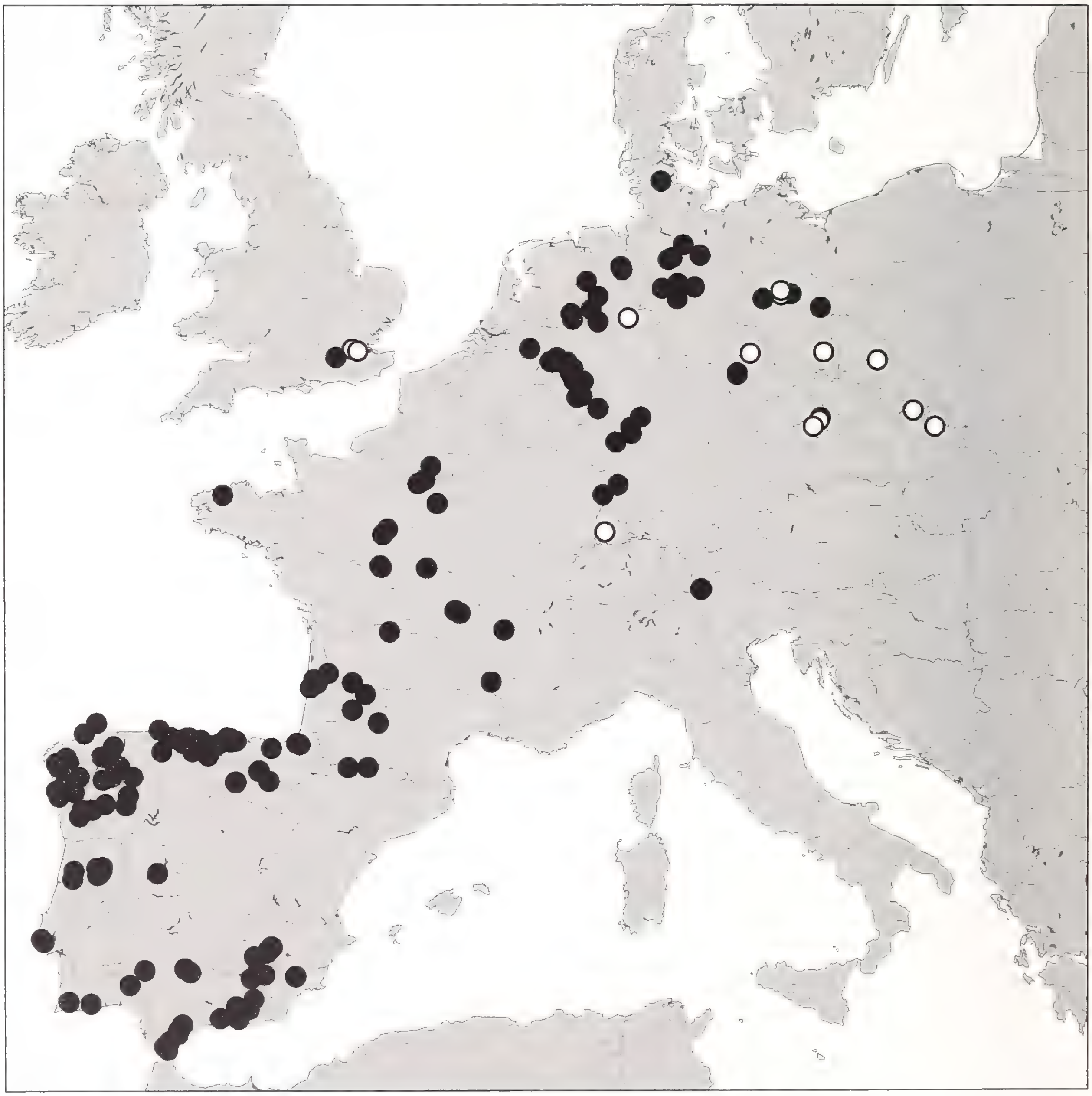
Adult specimens have been observed throughout the year (material examined). In pitfall trap studies in northwest German heathlands (Assing, unpubl.), teneral beetles were recorded in late summer and autumn (August through November). On two occasions, mature eggs were observed in the ovaries of females collected in May. Based on the material examined here, *M. piceus* is univoltine, not bivoltine as indicated by DRUGMAND (1989). Dissections of the thorax revealed that the flight muscles of most of the examined specimens from northern German heathlands were either rudimentary or absent (Assing, unpubl.) and that consequently only part of the populations is capable of flight. Records of flying specimens are from May and July (KÖHLER 2000; VOGEL 1979).

3.17. ***Medon cauchoisi* Jarrige, 1949**
(Figs. 79-84, Map 10)

Medon cauchoisi Jarrige, 1949 (JARRIGE 1949: 66).

Medon oculatior Peyerimhoff, 1949 (PEYERIMHOFF 1949: 249f) **syn. n.**

Medon lusitanicum Coiffait, 1970a (COIFFAIT 1970a: 715f) **syn. n.**



Map 9: Distribution of *Medon piceus* (Kraatz) (filled circles: revised records; open circles: selected literature records).

Medon parviphallus Coiffait, 1973b (COIFFAIT 1973b: 278ff) **syn. n.**

Medon mazices Coiffait, 1973b (COIFFAIT 1973b: 280ff) **syn. n.**

Medon fongondi Coiffait, 1980 (COIFFAIT 1980: 39f) **syn. n.**

Medon perraulti Coiffait, 1980 (COIFFAIT 1980: 41) **syn. n.**

Medon cribriceps Scheerpeltz i. l.

Types examined: *M. cauchoisi*: Holotype ♂: St M. du Canigou, P.O. VII.48 Dr. Ph. C. / TYPE / Muséum Paris Ex Collection J. JARRIGE 1976 / cauchoisi / Holotypus Medon cauchoisi Jarrige rev. V. Assing 2003 (MNHNP).

M. oculatior: Holotype ♂ [aedeagus missing]: O. el Akhdar pr. Tanant, Maroc, 28 juin 1923, Euphorbia serinifera [?] / TYPE / Medon oculatior Peyerimhoff, Type uniq. (MNHNP).

M. lusitanicus: Holotype ♂: PORTUGAL ALGARVE, ALGOZ, H. COIFFAIT -I.68 / MUSEUM PARIS COLL H. COIFFAIT / HOLOTYPE / Medon lusitanicum Coiff. H. COIFFAIT det. 1969 / Medon cauchoisi Jarrige det. V. Assing 2003 (MNHNP).

M. parviphallus: Holotype ♂: Maroc, Arbaoua, IV-72, H. C. / MUSEUM PARIS COLL H. COIFFAIT / HOLOTYPE / Medon parviphallus Coiff. H. COIFFAIT det. 1972 / Medon cauchoisi Jarrige det. V. Assing 2003 (MNHNP).

M. mazices: Holotype ♂: MAROC 22.4.72, QUEZZANE, H. COIFFAIT / MUSEUM PARIS COLL H. COIFFAIT / HOLOTYPE / Medon mazices H. COIFFAIT det. 1973 / Medon cauchoisi Jarrige det. V. Assing 2003 (MNHNP).

M. perraulti: Holotype ♂ [aedeagus missing]: St. Martin d´Albère / P.O. 26.III.70, G. Perrault / MUSEUM PARIS COLLECTION J. JARRIGE / TYPE / perraulti / Medon cauchoisi Jarrige det. V. Assing 2003 (MNHNP).

M. fongondi: Holotype ♂ [teneral]: Tizi n´Tchika, Ht Atlas, 9.V.67 / Maroc, H. Fongond / MUSEUM PARIS COLLECTION J. JARRIGE / TYPE / fongondi / Medon fongondi H. COIFFAIT 1978 / Medon cauchoisi Jarrige det. V. Assing 2003 (MNHNP).

Comments: The holotypes of *M. cauchoisi*, *M. oculatior*, *M. lusitanicus*, *M. parviphallus*, *M. mazices*, and *M. perraulti* are externally so similar that it seems most remarkable that they were described as different species. The aedeagus of *M. parviphallus* Coiffait is clearly teratologically malformed; for more details on such malformations see ASSING (2004a). An examination of the aedeagi and secondary sexual characters, as well as of the external characters of the other holotypes revealed no significant differences suggesting that they should represent distinct species. The teneral holotype of *M. fongondi* has a distinctly microsculptured head, but otherwise no evidence was found that it is specifically distinct from *M. cauchoisi*, neither in the external nor in the sexual characters. Consequently, *M. lusitanicus* Coiffait, *M. parviphallus* Coiffait, *M. mazices* Coiffait, *M. perraulti* Coiffait, and *M. fongondi* Coiffait are all placed in the synonymy of the senior name *M. cauchoisi*. Since *M. oculatior* and *M. cauchoisi* were described simultaneously and neither of the names has priority by publication date, *M. cauchoisi* is here designated as the senior name. (The original descriptions of both species were published in 1949; since there is no indication of the precise date, the publication date of both descriptions must be assumed to be December 31.)

Additional material examined (total: 405 exs.)**:**

Morocco: 4 exs., N-Morocco, Jbel Mousa, leg. Franz (NHMW, cAss); 2 exs., N-Morocco, Xauen, leg. Franz (NHMW, cAss); 1 ex., Rif, Xauen, Puente Fomento, 30.III.1959, leg. Besuchet (cBor); 3 exs., Rif, Dardara, near Xauen, 30.III.1959, leg. Besuchet (MHNG); 2 exs., Rif, Mt. Lexchab, 1.IV.1959, leg. Besuchet (MHNG); 1 ex., Moyen Atlas, Afourer, leg. Franz (cAss); 2 exs., Jebel Tazeka, Taza, leg. Franz (NHMW, cAss); 2 exs., M. de Kebdana, 30 km NW Berkane, 35°03N, 02°36W, 350 m, 31.XII.2001, leg. Bayer (cSch); 1 ex., Rif, 15 km SW Zinat, Tieta-des Beni-Yda-Cherki, 570 m, oak forest, 14.II.2003, leg. Wrase (cSch); 2 exs., Tanger (DEI, IRSNB); 1 ex., Tanger, XII.1894 (MHNG); 3 exs., Oued Sebou near Kenitra, V.1961, leg. Comellini (MHNG); 1 ex., Oued Sebou, IV.1961, leg. Comellini (cAss); 3 exs., 10 km N Larache, Jemis del Sahel, 8.V.1960, leg. Besuchet (MHNG); 1 ex., Jemis del Sahel, leg. Franz (NHMW); 4 exs., Ceuta [35°53N, 05°20W], leg. Comellini (MHNG, cAss).

Portugal: 1 ex., Algarve, Tavira, Alcaria do Cume, 37°15N, 07°44W, 440 m, 12.IV.2002, leg. Meybohm (cAss); 1 ex., Algarve, Serra de Monte Figo, 37°06N, 07°48W, 200 m, 4.IV.2001, leg. Meybohm (cAss); 5 exs., Algarve, Serra de Cume, Alcaria, 37°14N, 07°43W, 420 - 430 m, 31.III.2001, leg. Meybohm (cAss); 23 exs., Algarve, 10 km N S. Brás de Alportel, 400 m, 4.VI.1992, leg. Wunderle (cAss); 1 ex., N Alportel, 37°11N, 07°55W, 340 m, 4.IV.2002, leg. Meybohm (cAss); 4 exs., Algarve, N Faro, Freixo-Seco, 37°16N, 08°03W, 440 m, 9.IV.2001, leg. Meybohm (cAss); 2 exs., Algarve, Rocha da Pena, N-slope, 37°15N, 08°05W, 9.IV.2001, leg. Meybohm (cAss); 2 exs., Algarve, N Loulé, Querenca, Fonte Benemola, 37°12N, 08°00W, 150 m, 5.IV.2002, leg. Meybohm (cAss); 12 exs., Algarve, Monchique, above road to Alferce, 37°19N, 8°32W, 590 m, 10.IV.2002, leg. Meybohm (cAss); 31 exs., Caldas de Monchique, V-VI.1960, leg. Fagel (IRSNB); 2 exs., Faro, Silves, leg. Franz (NHMW); 2 exs., Faro, Azinhal, 14.V.1994, leg. Bayer & Winkelmann (cSch).

Spain: Cataluña: 1 ex., Granollers, La Roca, leg. Franz (cAss); 6 exs., 40 km N Barcelona, Sierra de Montseny, 700 m, S-slope, 19.III.1994, leg. Assing, Wunderle (cAss, Wun); 1 ex., Sierra de Montseny, Santa Fe, leg. Franz (NHMW); 5 exs., Sierra de Montseny, leg. Franz (NHMW); 1 ex., Barcelona, Vallirana, leg. Franz (NHMW); 1 ex., Barcelona (MHNG); 3 exs., Barcelona, Montsenat, 3.IV.1956, leg. Coiffait (MHNG); 2 exs., Barcelona, Puerto Ordal, 22.III.1959, leg. Besuchet (MHNG); 2 exs., Gerona, Ripoll, 11.III.1978 (cAss); 2 exs., Gerona, Puerto de Collsuspina, leg. Franz (NHMW); 2 exs., Gerona, Tapis, 1000 m, 28.II.1997, leg. Tonquet (cTro); 2 exs., Arampruya, Begas, leg. Franz (NHMW); 3 exs., Gerona, Ripoll, 11.III.1978 (MHNG). **Madrid:** 3 exs., Sierra Guadarrama, Escorial, leg. Franz (NHMW). **Aragón:** 3 exs., 20 km SE Teruel, La Puebla de Valverde, 40°13N, 00°57W, 1100 m, 14.IV.2003, leg. Assing (cAss); 8 exs., 50 km ESE Teruel, N Rubielos de Mora, 40°14N, 00°37W, 1255 m, oak forest, 13.IV.2003, leg. Assing (cAss); 1 ex., 30 km S. Teruel, Sierra del Javalambre, NE Javalambre, 40°09N, 01°00W, 1700 m, 14.IV.2003, leg. Assing (cAss); 5 exs., WNW Teruel, Sierra de Albarracín, Orihuela d. T., 40°32N, 01°40W, 1520 m, 12.IV.2003, leg. Assing (cAss); 1 ex., Huesca, Sierra de Alcubierre, leg. Franz (NHMW). **Castilla-La Mancha:** 2 exs., Cuenca, 9.IV.1887, leg. Korb (DEI, NHMW); 1 ex., 90 km N Montoro, Sierra del Rey, Puerto de Niefla, 38°32N, 04°22W, 850 m, oak forest, 28.XII.2003, leg. Assing (cAss). **Valencia:** 2 exs., Serra, leg. Franz (NHMW); 1 ex., Alicante, Sierra de Bernia, 19.III.1978, leg. Meybohm (MHNG); 1 ex., Castellón, Cervera del Maestre, 13.V.1966, leg. Besuchet (MHNG). **Murcia:** 2 exs., Sierra de Espuña, leg. Franz (NHMW); 4 exs., Sierra de Espuña, 26.III.1959, leg. Besuchet (MHNG). **Andalucía:** 7 exs., Ronda, Sierra de Grazalemma (CA), Puerto las Palomas, 1000 m, 25.III.1994, leg. Assing, Wunderle (cAss, cWun); 1 ex., Sierra de Grazalemma, 1100 m, 1.X.1993, leg. Wunderle (cSch); 2 exs., Malaga, leg. Franz (NHMW); 1 ex., SE Ronda, Sierra de Palmitera (MA), 900 m, 24.III.1994, leg. Assing (cAss); 12 exs., Ronda, Sierra de Ubrique (CA), 1000 m, 25.III.1994, leg. Assing, Wunderle (cAss, cWun); 1 ex., Ubrique, 600 m, 2.X.1993, leg. Wunderle (cWun); 1 ex., Sierra de Ronda, Mte. Arastepa, leg. Franz (NHMW); 2 exs., Sierra de Bermeja, M. Los Reales, 1450 m, 26.III.1994, leg. Assing (cAss); 10 exs., Sierra de Bermeja, Jubrique, 350 m, 26.III.1994, leg. Assing, Wunderle (cAss, cWun); 1 ex., Sierra de Bermeja, 1000 m, 26.III.1994, leg. Assing (cAss); 1 ex., Sierra de Bermeja, Puerto de Peñas Blancas, 1200 m, 26.III.1994, leg. Wunderle (cWun); 1 ex., N Algeciras, 36°15N, 05°26W, moist forest, 21.II.2000, leg. Lompe (cAss); 18 exs., Algeciras, Sierra de Luna (CA), 200 - 350 m, 28.III.1994, leg. Assing, Wunderle (cAss, cWun); 6 exs., Sierra de Luna, 27.V.1966, leg. Besuchet, Comellini (MHNG); 1 ex., 8 km E Tarifa, Mirador del Estrecho, 36°03N, 05°33W, 310 m, under palm trees and bushes, 10.II.1999, leg. Zerche (DEI); 1 ex., 10 km W Los Barrios, 36°11N, 05°34W, 210 m, leaf litter below cork trees, 10.II.1999, leg. Zerche (DEI); 4 exs., Cadiz, 14 km NE Alcalá de los Gazules, 36°32N, 05°39W, 430 m, cork tree forest, 2.II.1999, leg. Zerche (DEI); 5 exs., Algeciras, Sierra de Fates (CA), 350 m, 28.III.1994, leg. Assing, Wunderle (cAss, cWun); 1 ex., Algeciras, leg. Quedenfeldt (NHMW); 1 ex., Algeciras, 1./2.V.1956, leg. Fagel (IRSNB); 2 exs., Algeciras, leg. Fauvel (IRSNB, NHMW); 2 exs., Algeciras, Cerro de Mirador, leg. Franz (NHMW); 4 exs., Sierra de Aracena, Acebuches, 37°53N, 06°48W, 5.IV.2001, leg. Meybohm (cAss); 2 exs., Cádiz, El Bujeo, 36°04N, 05°32W, 230 m, oak forest, 9.IV.2001, leg. Sprick (cAss); 3 exs., Cadiz, Pto. de Bujeo, 30.V.1966, leg. Besuchet (MHNG); 1 ex., Cádiz, Los Barrios, 22.IV.1960, leg. Besuchet (cAss); 1 ex., Tarifa, Puerto de Ojén, 19.III.2002, leg. Aßmann (cAss); 1 ex., Tarifa, leg. Franz (NHMW); 2 exs., Sierra de Cordoba, leg. Franz (NHMW); 1 ex., N Sevilla, Sierra Morena, leg. Franz (NHMW); 1 ex., Sierra de Cazorla, source of Gualaquivir river, 1200 m, 6.X.1993, leg. Wunderle (cWun); 2 exs., Sierra de Cazorla, leg. Franz (NHMW); 2 exs., Sierra de Cazorla, 12.IV.1959, leg. Besuchet (cBor); 1 ex., W Lanjaron, Alpujarra, 1400 m, 23.III.1994, leg. Wunderle (cWun); 3 exs., Marbella, 1964, leg. Frey (NHMW); 2 exs., Sierra Nevada, Laroles, 300m, 22.III.1987, leg. Zoia (cZan); 2 exs., Vejer de la Frontera (CA), 27.III.1987, leg. Zoia (cZan); 4 exs., Malaga, Montes des Malaga, 28.III.1959, leg. Besuchet (MHNG); 4 exs., Malaga, 4 km NW Yunquera, 36°40N, 04°57W, 725 m, 1.II.1999, leg. Zerche (DEI); 13 exs., 15 km NNE Málaga, Montes de Málaga, 36°48N, 04°23W, 750 m, bank of stream with *Salix*, etc., 24.XII.2003, leg. Assing (cAss); 15 exs., 15 km NNE Málaga, Montes de Málaga, 36°48N, 04°22W, 900 m, mixed pine and corktree forest, 24.XII.2003, leg. Assing (cAss); 6 exs., 15 km NE Málaga, Montes de Málaga, 36°47N, 04°21W, 900 m, N-slope with *Quercus suber*, 24.XII.2003, leg. Assing (cAss); 1 ex., ca. 20 km S Loja, 5 km NW Zafarraya, 36°59N, 04°10W, 900 m, *Quercus ilex* forest, 24.XII.2003, leg. Assing (cAss); 23 exs., ca. 30 km NW Córdoba, E Villaviciosa, 38°05N, 04°54W, ca. 300 m, corktree forest, 28.XII.2003, leg. Assing (cAss); 4 exs., ca. 30 km NW Córdoba, E Villaviciosa, 38°05N, 04°53W, ca. 500 m, corktree litter at roadside, 28.XII.2003, leg. Assing (cAss); 4 exs., 60 km N Montoro, N Azuel, 38°19N, 04°19W, ca. 600 m, N-slope with scattered corktrees and shrubs, litter and grass roots sifted, 28.XII.2003, leg. Assing (cAss); 1 ex., locality not specified (NHMW).

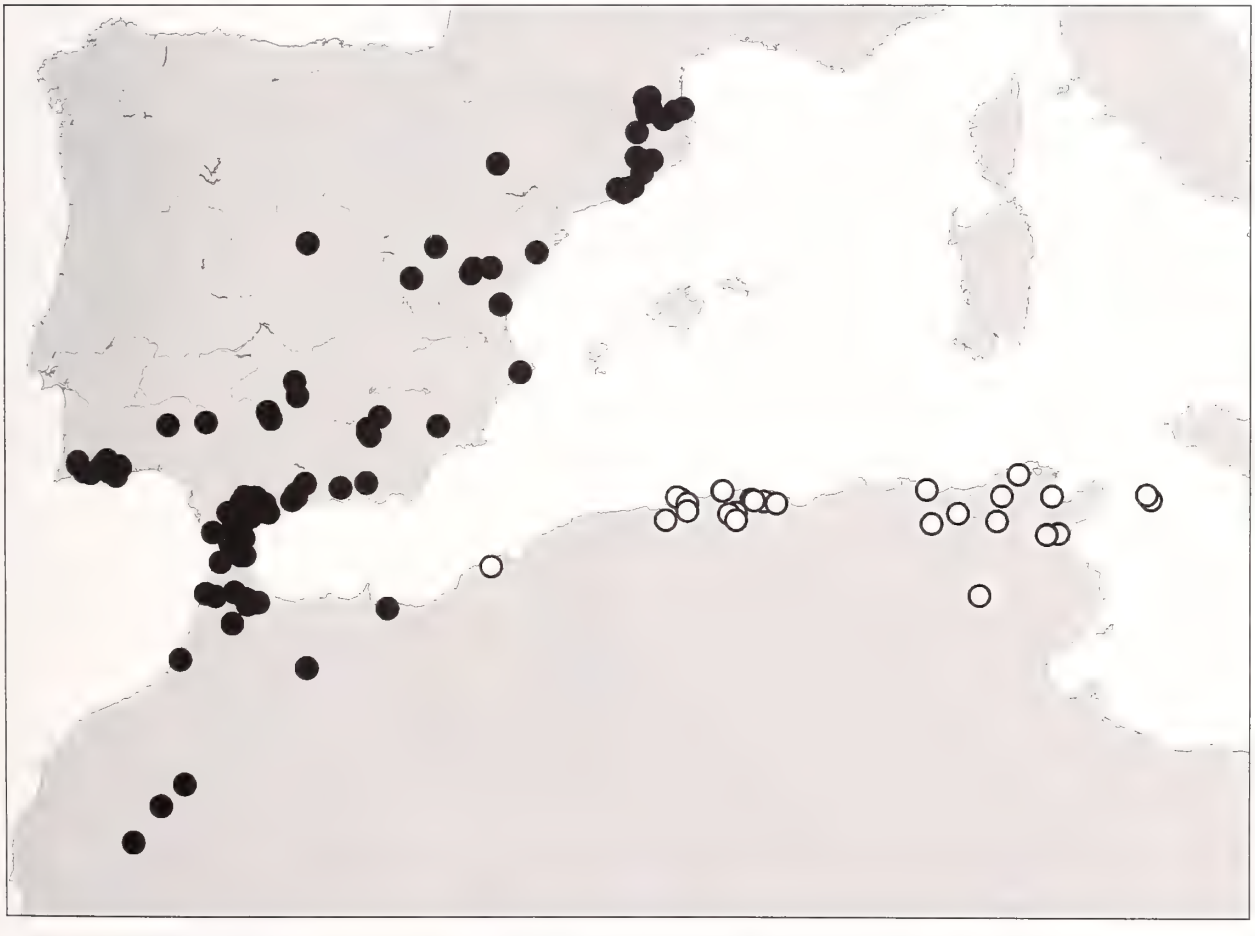
Gibraltar: 8 exs., The Upper Rock Nature Reserve, 36°09N, 05°21W, 350 m, leaf litter under bushes, 5.II.1999, leg. Zerche (DEI).

France: Languedoc-Roussillon: 2 exs., Vernet les Bains, Rte. de Sahorre, 700 m, 17.VI.1999, leg. Wolf (cSch); 1 ex., Molitg les Bains, 500 m, sifted from dry plants, 22.XI.1996, leg. Tronquet (cTro); 1 ex., same data, but 30.III.2001 (cTro); 1 ex., Molitg les Bains, 600 m, 13.VI.1995, leg. Tronquet (cTro); 1 ex., Molitg les Bains, 550 m, sifted moss, 22.II.1997, leg. Tronquet (cTro); 2 exs., Molitg les Bains, 22.II.2002, leg. Tronquet (cTro); 1 ex., Campôme, 1250 m, 9.IV.1999, leg. Tronquet (cTro); 1 ex., Campôme, 700 m, 13.IV.2001, leg. Tronquet (cTro); 4 exs., Collioure, 250 m, 3.XII.1999, leg. Tronquet (cTro); 4 exs., Collioure, 7.I.2000, leg. Tronquet (cTro); 1 ex., Fenouillet, gorges de Saint-Jaume, 11.XI.2002, leg. Tronquet (cTro); 4 exs., Corneilla-de-Conflent, 800 m, *Quercus ilex* litter, 25.III.2000, leg. Tronquet (cTro).

Diagnosis: 3.5 - 4.5 mm. Habitus as in Fig. 79. Coloration somewhat variable; usual coloration: castaneous to blackish brown, with the head usually slightly darker than pronotum and elytra; legs and antennae testaceous yellowish brown, with the basal antennomeres usually reddish brown to ferrugineous.

Head of variable shape, usually at least weakly oblong, rarely about as wide as long; temples behind eyes subparallel or weakly converging; eyes moderately large, in dorsal view slightly shorter than half the length of postocular region; puncturation coarse, dense, and well-defined, interstices reduced to narrow ridges or nearly so; occasionally in median dorsal area with small spot with slightly sparser puncturation; interstices usually without microsculpture and shining, sometimes with shallow microsculpture in posterior part of head, or very rarely microsculptured everywhere and matt (Fig. 80).

Pronotum approximately as wide as long and usually slightly narrower than head; puncturation variable, as coarse and dense as that of head or somewhat finer and sparser; median line without punctures; microsculpture absent (Fig. 80).



Map 10: Distributions of *Medon cauchoisi* Coiffait (filled circles) and of *M. despectus* (Fairmaire) (open circles) in the Western Mediterranean, based on examined records only.

Elytra of variable length and width, usually approximately 1.2 times as wide as and at suture at least slightly longer than pronotum (Fig. 79)

♂: protarsomeres I - IV not dilated; posterior margin of sternite VII shallowly concave and laterally with combs of 6-10 (mostly 8) palisade setae (Fig. 81); posterior incision of sternite VIII not very deep. Aedeagus as in Figs. 82-84, central area of ventral process in cross-section concave.

Comparative notes: Among most of its Western Mediterranean congeners, *M. cauchoisi* is readily identified by the coarse, dense, and well-defined puncturation of the head and the pronotum. Regarding the puncturation of the head, the species is similar to *M. brunneus*, which, however, differs by its usually larger size, its larger and usually not oblong head, the narrower and shorter elytra, and especially by the morphology of the aedeagus. In *M. mirei*, the head is relatively larger, of subcircular shape, and less shining, the elytra are much shorter and narrower, the hind wings are reduced, the palisade fringe at the posterior margin of the abdominal tergite VII is reduced, and the aedeagus is of different morphology.

Distribution and bionomics: *Medon cauchoisi* is an Atlanto-Mediterranean element (Map 10), its distribution including Morocco, southern Portugal, the southern, central, eastern, and northeastern parts of Spain, and the Pyrénées-Orientales in southwestern France. Interestingly, it is apparently absent from the northwestern half of the Iberian Peninsula, where *M. piceus* is common. Similarly, there is only little overlap of the range of *M. cauchoisi* and that of the closely related *M. brunneus* (Map 8) in northeastern Spain (Cataluña) and southwestern France (Pyrénées-Orientales). The distributions of *M. cauchoisi* and *M. despectus*, another closely allied species, are apparently strictly allo- or parapatric (Map 10).

M. cauchoisi has been collected in a wide range of – usually forest – habitats, mostly in the leaf litter of various species of oak, but also from debris below palm trees and bushes, and from moss. Adult beetles were found during the period from October through June, but the absence of records from the period July to September may also be due to low collecting activity in the region where *M. cauchoisi* occurs.

3.18. *Medon despectus* (Fairmaire, 1860)
(Figs. 85-89, Map 10)

Lithocharis despecta Fairmaire, 1860 (FAIRMAIRE 1860: 160).

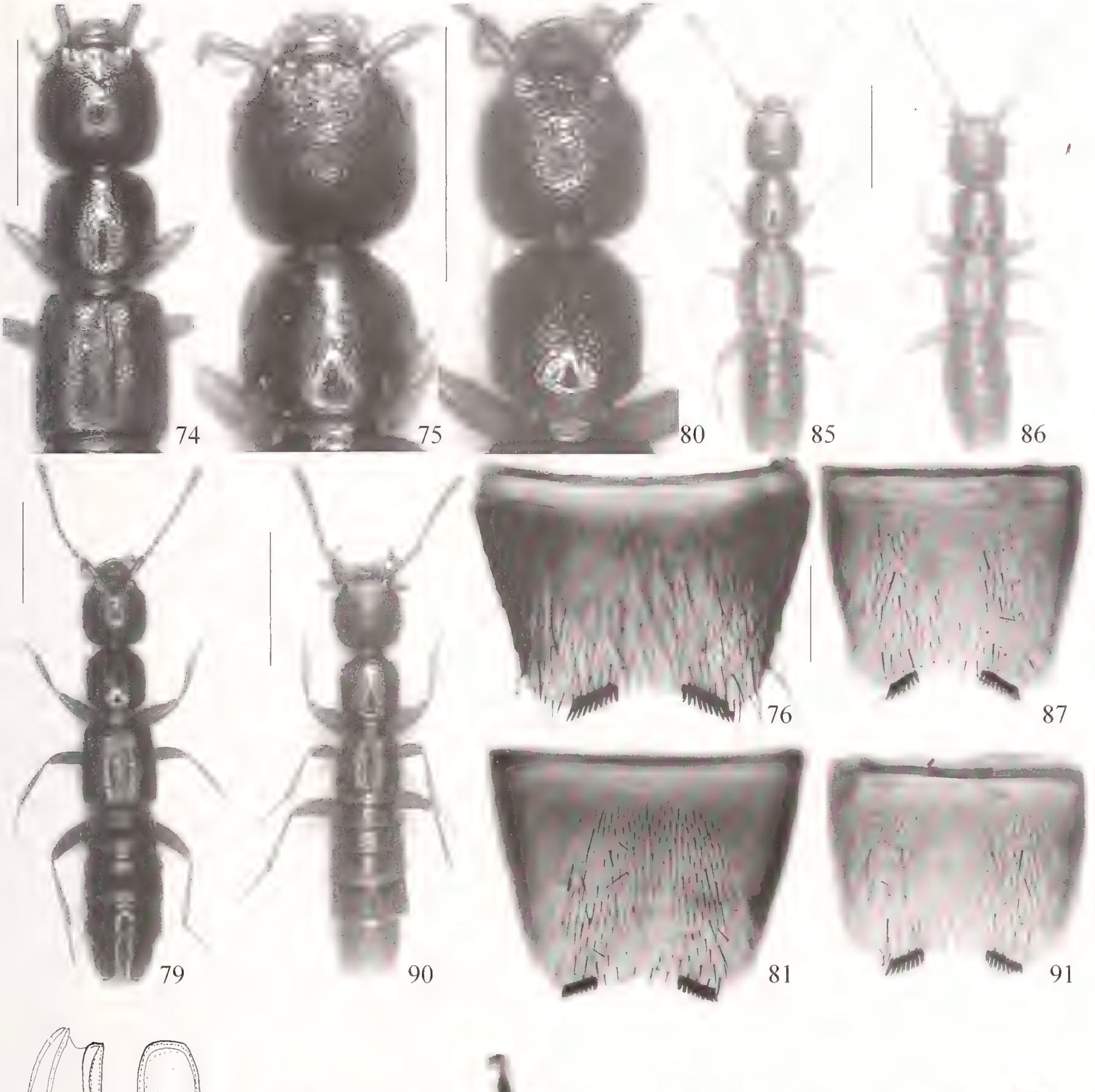
Type examined: Syntype ♀: Philippeville / Syntype / despecta Fairm / Coll. A. Fauvel, R.I.Sc.N.B.17.819 / Medon despectus (Fairmaire) det. V. Assing 2003 (IRSNB).

Additional material examined (total: 168 exs.):

Tunisia: 1 ex., SW Zaghouan, Jebel Zaghouan, 36°22N, 10°07E, 800 m, N-slope, litter and grass sifted, 29.XII.2004, leg. Assing (cAss); 3 exs., ca. 25 km SW El Fahs, 36°15N, 09°48E, 340 m, reservoir, stream valley with poplar etc., moss and litter sifted, 25.XII.2004, leg. Wunderle (cWun); 1 ex., Falnassa, 15 km N Beja, 500 m, 1.X.1995, leg. Schulz & Vock (cAss); 4 exs., "Tunis", leg. Fauvel (NHMW, cAss); 1 ex., El Feidja (NHMW); 1 ex., Kasserine, X.1937, leg. Demofys (cTro); 31 exs., 25 km W Jendouba, ca. 10 km N Ghardimaou, Ain Soltane, 36°29N, 08°19E, 670 m, litter of oak forest, 27.XII.2004, leg. Assing (cAss); 20 exs., same data, but 600 m, 28.XII.2004, leg. Assing (cAss); 4 exs., NW-Tunisia, Ghardimaou Forest, El Feidja, 700 m, 13.IV.1989, leg. Meregalli (DEI, cAss); 1 ex., Feidja, Aïn Soltane, 700 m, 13.IV.1989, leg. Meregalli (DEI); 1 ex., Teboursouk (IRSNB).

Algeria: 1 ex., El Biar, III.1909 (NHMW); 1 ex., Temmapes (?), leg. Théry (cAss); 1 ex., Bols de Bainen, III.1909 (cAss); 3 exs., St. Charles, leg. Théry (IRSNB, NHMW); 1 ex., Algier (DEI); 2 exs., Algier (MHNG, cAss); 1 ex., Laverdure, 6.X.1929, leg. Schatzmayr (UCBA); 1 ex., Bône (IRSNB); 1 ex., Bou Berak, near Dellys (IRSNB); 5 exs., Grand Kabylie, Azazga – Yakouren, 600 m, 14.V.1988, leg. Besuchet, Löbl & Burckhardt (MHNG, cAss); 14 exs., Grande Kabylie, Forêt d´Akfadou, 26 km E Yakouren, 1200 m, 16.V.1988, leg. Besuchet, Löbl & Burckhardt (MHNG, cAss); 1 ex., Grande Kabylie, Yakouren, 730 m, 12.V.1988, leg. Besuchet, Löbl & Burckhardt (MHNG); 2 exs., Oued Sébaou, W Dellys, 20.V.1988, leg. Besuchet, Löbl & Burckhardt (cAss); 4 exs., Grande Kabylie, l´Arbatache sur El Kseur, 300-400 m, 18.V.1988, leg. Besuchet, Löbl & Burckhardt (MHNG, cAss); 13 exs., Grande Kabylie, Oued Aissi, Ouadhia, 200 m, 12.V.1988, leg. Besuchet, Löbl & Burckhardt (MHNG, cAss); 13 exs., Grande Kabylie, Djebel Bou-Berak, 350 m, 19.V.1988, leg. Besuchet, Löbl & Burckhardt (MHNG, cAss); 2 exs., Djurdjura, sur Boghni, 11.V.1988, leg. Besuchet, Löbl & Burckhardt (MHNG); 8 exs., Djurdjura, 4 km SW Tikjda, 1200 m, 7.V.1988, leg. Besuchet, Löbl & Burckhardt (MHNG, cAss); 5 exs., Gorges de la Chiffa, Ruisseau des Singes, 280 - 380 m, 4.V.1988, leg. Besuchet, Löbl & Burckhardt (MHNG, cAss); 3 exs., Larba, 180 m, 4.V.1988, leg. Besuchet, Löbl & Burckhardt (MHNG, cAss).

Italy: 14 exs., Pantelleria, Mte. Gibelè, 600m, 12.IX.1986, leg. Sette (cZan, cAss); 2 exs., Pantelleria, II.1913, leg. Dodero (DEI).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Figs. 74-94. *Medon piceus* (Kraatz) (74-78), *M. cauchoisi* Jarrige (79-84; 84: holotype), *M. despectus* (Fairmaire) (85-89), and *M. mirei* Coiffait, holotype (90-94): forebody (74); head and pronotum (75, 80); habitus (85, 86, 79, 90); male sternite VII (76, 81, 87, 91); aedeagus in lateral and in ventral view (77-78, 82-84, 88-89, 92-94). Scale bars: 74-75, 79-80, 85-86, 90: 1.0 mm; 76-78, 81 -84, 87-89, 91-94: 0.2 mm.

Locality not specified or ambiguous: 1 ex. (IRSNB); 1 ex., with several locality labels (IRSNB).

Diagnosis: External characters as in *M. cauchoisi*, except for the paler average coloration, the slightly lower average size, and the mostly shorter elytra (Figs. 85-86). Wing-dimorphic species; elytra at suture in macropterous specimens 1.05 - 1.10 times as long as pronotum (Fig. 85), in submacropterous specimens approximately as long as pronotum (Fig. 86).

♂: secondary sexual characters as in *M. cauchoisi* (Fig. 87). Aedeagus smaller and more slender than in *M. cauchoisi*, apically rounded both in lateral and in ventral view (Figs. 88-89).

Comparative notes: Among Western Mediterranean *Medon*, *M. despectus* is most similar to *M. cauchoisi*, from which it is reliably separated only by the different shape of the aedeagus. *Medon mirei*, which, too, occurs in Northwest Africa, has much smaller eyes, completely reduced hind wings, and it lacks the palisade fringe at the posterior margin of the abdominal tergite VII. From the closely related, highly variable *M. semiobscurus* (Fauvel) from the Eastern Mediterranean, whose aedeagus has a similar shape, *M. despectus* is distinguished by lower average size, shorter antennae with shorter and less oblong antennomeres III - VI, as well as by a smaller and less massive aedeagus.

Distribution and bionomics: The known distribution of this species is confined to Tunisia, Algeria, and the Italian island Pantelleria (Map 10), from where it was previously recorded as *M. brunneus* (CICERONI & ZANETTI 1995). For some additional records see NORMAND (1935). The material examined was collected at altitudes of 180-1200 m in autumn (September, October), winter (December, February), and in spring (March through May). At least 52 Tunisian specimens were sifted from the leaf litter of an oak forest.

3.19. ***Medon mirei*** **Coiffait, 1980** (Figs. 90 - 94)

Medon mirei Coiffait, 1980 (COIFFAIT 1980: 40f).

Medon giachinoi Bordoni, 1988 (BORDONI 1988: 343ff) **syn. n.**

Types examined: *Medon mirei*: Holotype ♂: Ft. de Guerrouch, Alg. P. de Mire / TYPE / Muséum Paris Ex Collection J. Jarrige 1976 / Fagete / Medon mirei H. Coiffait 1979 (MNHNP).

Medon giachinoi: Holotype ♂: Algeria – Juel, F.t de Guerrouch, 4/10 – XI – 1984 / M. R. S. N. Spedizione "Algeria ´84" Boffa – Casale – Cavazzuti – Gavetti – Giachino – Levi / Holotypus / Medon giachinoi Bordoni det. 1987 / Medon mirei Coiffait det. V. Assing 2003 (MRSNT). Paratypes: 12 exs.: same data as holotype (MRSNT, cBor, cAss).

Comments: The locality on the label of the type specimen of *M. mirei* is not identical with the type locality indicated in the original description: "gorges de Kedaia, Algérie" (COIFFAIT 1980). The description and the collector, however, are in agreement with the above type specimen, and Coiffait´s citation of type labels is not always reliable (see *M. siculus*).

The original description of *M. giachinoi* is based on 23 specimens collected in the same locality as the holotype of *M. mirei*. As was expected, the examination of the holotype and 12 paratypes of *M. giachinoi* revealed that it is conspecific with the holotype of *M. mirei*; hence the synonymy indicated above. BORDONI (1988) compares *M. giachinoi* with various congeners, but does not mention *M. mirei*.

Diagnosis: Small species, 3.3 mm. Habitus as in Fig. 90. Coloration uniformly ferrugineous, appendages testaceous.

Head of almost subcircular shape, approximately as wide as long; eyes of distinctly reduced size, in dorsal view about one fourth the length of postocular region, and not projecting from lateral outline of head; punctuation coarse, dense, and areolate; interstices reduced to narrow ridges and microsculptured; dorsal surface matt.

Pronotum distinctly narrower than head, approximately 0.9 times its width, and slightly longer than wide; puncturation coarse, dense, areolate, and partly confluent; interstices and median line with distinct shine, microsculpture absent.

Elytra only slightly wider (about 1.1 times) than and at suture only 0.75 times as long as pronotum; puncturation moderately dense; interstices distinctly shining. Hind wings reduced. Palisade fringe at posterior margin of abdominal tergite VII reduced.

♂: posterior margin of sternite VII of similar shape and chaetotaxy as in *M. cauchoisi* (Fig. 91); sternite VIII posteriorly with rather broad and not very deep emargination. Aedeagus of similar general morphology (shape and internal structures) as in *M. cauchoisi*, but in ventral view apically with converging lateral margins and without subapical dilatation, and in lateral aspect apically rounded (Figs. 92-94).

Comparative notes: *Medon mirei* is readily distinguished from its Western Palaearctic congeners by the small eyes, the small body size, the short elytra and reduced hind wings, and by the male sexual characters.

Distribution and bionomics: The species is known only from the type locality in Algeria. The adaptive reductions of eye size, pigmentation, and wings suggest that it has a subterranean habitat.

3.20. *Medon fusculus* (Mannerheim, 1830) (Map 11)

Rugilus fusculus Mannerheim, 1830 (MANNERHEIM 1830: 40).

Lithocharis fusculus Lacordaire, 1835 (LACORDAIRE 1835: 431).

Lithocharis testaceus Lacordaire, 1835 (LACORDAIRE 1835: 432).

Lithocharis rufus Mulsant & Rey, 1853 (MULSANT & REY 1853: 66).

Lithocharis auranitica Saulcy, 1864 (SAULCY 1864: 40).

Lithocharis infuscatus Baudi, 1870 (BAUDI 1870: 392).

Medon deficiens Hubenthal, 1911 (HUBENTHAL 1911: 188).

Medon abchasicus Bernhauer, 1922 (BERNHAUER 1922: 124).

Medon bulgaricus Coiffait, 1970b (COIFFAIT 1970b: 105f).

Medon gajaci Coiffait, 1973a (COIFFAIT 1973a: 114ff).

Medon paradobrogicus Decu & Georgescu, 1994 (DECU & GEORGESCU 1994: 49f).

Types examined: See ASSING (2004a).

Additional material examined (total: 216 exs.; for additional material examined see ASSING (2004a))**:**

France: Aquitaine: 2 exs., Gironde, Cambes, 18.XII.1936, leg. Giraud (MHNG, cAss); 3 exs., Cambes, 20.XI.1936 MHNG). **Picardie:** 1 ex., Oise, Laigneville, IX.1908, leg. Mequignon (MHNG); 11 exs., Laigneville, 24.IV.1924 (MHNG); 1 ex., Laigneville (MHNG); 2 exs., Oise, Noyon, leg. de Brunier (MHNG). **Champagne-Ardenne:** 2 exs., Les Grandes Loges (MHNG); 2 exs., Les Grandes Loges, VIII.1918 (MHNG). **Île-de-France:** 1 ex., Fontainebleau (MHNG). **Rhône-Alpes:** 1 ex., Haute-Savoie, Malagny, 14.XII.1963, leg. Comellini (MHNG); 1 ex., Rhône, Irigny, Rhône inundation, XII.1954 (MHNG); 1 ex., Isère, Grenoble, 12.VII.1902 (MHNG); 1 ex., Ain, Poncin, I.1948 (MHNG). **Alsace:** 2 exs., Strasbourg, VIII.1953, IV.1954 (MHNG). **Lorraine:** 2 exs., Metz (MHNG). **Locality not specified, ambiguous, or not identified:** 2 exs., locality not specified (NHMW); 1 ex., "IN Cendrieux Bourlet", III.1960 (MHNG); 1 ex., "Cussac" (MHNG).

England: 1 ex. [aedeagus and male sternite VII teratological], East Sussex, Rye, 14.II.1999, leg. Hance (cOwe).

Italy: Friuli-Venezia Giulia: 1 ex., Villotta, 19.II.1973, leg. Zanetti (cBor); 1 ex., W Carnia, bank of Fella river, 45°23N, 13°07E, 250 m, flood debris, 12.IX.1998, leg. Schülke (cSch); 2 exs., bank of Isonzo river SE Villesse, 45°51N, 13°27E, 10 m, flood debris, 13.IX.1998, leg. Schülke (cSch); 2 exs., Villotta (PN), 19.II.1973, leg. Zanetti (UCBA, cZan); 3 exs., Sacile (PN), mole nest, 6.III.1974, leg. Osella & Zanetti (cZan); 5 exs., Gemona del Friuli (UD), mole nest, 6.III.1974, leg. Osella & Zanetti (cZan); 1 ex., Monfalcone, 21.III.1948, leg. Springer (UCBA); 1 ex., Udine (MHNG).

Germany: Niedersachsen: 1 ex., Hameln, Königsförde, garden, V.1988, leg. Sprick (cAss). **Nordrhein-Westfalen:** 1 ex. [with worker of *Lasius brunneus* attached to the pin], Kölner Bucht, Pulheim, Stommelerbusch, 4.V.1984, leg. Köhler (cKöh). **Rheinland-Pfalz:** 2 exs., Bacharach, bank of Rhine river, flood debris, I-II.2001, leg. Hetzel (cFel); 3 exs., Bacharach, Steeg, vineyard, 56.VI.1996, leg. Köhler (cKöh); 1 ex., same data, but 14.VII.1996 (cKöh); 2 exs., Oppenheim, 14.X.1989, leg. Höhner (cKöh); 1 ex., Schloßböckelheim, 25.IV.1994, leg. Köhler (cKöh); 3 exs., same data, but 31.V.1996; 1 ex., same data, but 28.VII.1996 (cKöh); 2 exs., Monzingen, 18.-19.V.1991, leg. Köhler (cKöh). **Baden-Württemberg:** 1 ex., Kaiserstuhl, Durbach, 14.VII.1971 (MHNG). **Hessen:** 1 ex., Groß-Gerau, 6.II.1988, leg. Höhner (cKöh). **Berlin/Brandenburg:** 13 ex., Rüdersdorf, Kalkberge (DEI, cSch); 1 ex., Glambeck (DEI); 9 exs., Berlin, Hohen Neuendorf (DEI); 4 exs., Oderberg (DEI).

Austria: Vorarlberg: 1 ex., Feldkirch (NHMW). **Niederösterreich/Wien:** 27 exs., Wien, several localities (DEI, MHNG, NHMW); 6 exs., Wiener Wald, Rüdersdorf (NHMW); 1 ex., Wien, Donauauen, 29.XI.1952, leg. Malicky (MHNG); 4 exs., Stockerau (NHMW); 1 ex., Albern (NHMW); 1 ex., Metzendorf (NHMW); 1 ex., Rodaun (NHMW); 1 ex., Mödling, Eichkogel (NHMW); 1 ex., Laxenburg (NHMW); 1 ex., Bisamberg (NHMW); 4 exs., Bisamberg, 27.III.1953, leg. Malicky (MHNG); 1 ex., Ulrichskirchen (NHMW); 1 ex., Wechselgebiet (NHMW). **Steiermark:** 1 ex., Graz (MHNG); 1 ex., "Süd-Steiermark" (NHMW).

Czech Republic: 10 exs., Moravia, Bulhary, 25.VI.1984, leg. Prudek (cSch, cAss).

Bulgaria: 1 ex., Asenovgrad (MHNG).

Croatia: 1 ex., Mlini [42°37N, 18°12], 29.IX.-4.X.1958, leg. Benick (MHNG); 3 exs., Brela [43°22N, 16°56E], 16.-26.IX.1958, leg. Benick (cAss).

Bosnia-Herzegovina: 1 ex., Montenegro, Budva, leg. Hummler (MHNG); 4 exs., Montengro, Herzeg-Novi (MHNG).

Serbia-Montenegro: 1 ex., Zvonačka Banja, 28.IV.2002, leg. Hlaváč (cAss).

Greece: 8 exs., Voiotia, Levadia, wet moss, 4.IX.1964, leg. Puthz (MHNG); 2 exs., Makedhónia, Nomós Kavála, 10 km W Eleftherópoli, Pangéo, 900 m, beechforest, 10.IV.1994, leg. Schawaller (SMNS); 2 exs., Makedhónia, Nomós Kavála, 10 km N Paleá Kavála, 600 m, macchia & chestnut forest, 20.IV.1994, leg. Schawaller (SMNS, cAss); 1 ex., Makedhónia, Nomós Kavála, Nestos delta S Khrisópoli, floodplain forest, 26.IV.1994, leg. Schawaller (SMNS); 2 exs., Thrakia, Nomós Xánthi, Nestos near Toxótes, 25.IV.1994, leg. Schawaller (SMNS, cAss); 3 exs., Pelopónnisos, Kalavrita, 800 m, 3.IV.1971, leg. Löbl (MHNG); 1 ex., Pelopónnisos, Taygetos, Meligalás, Dhervénion, 600 m, 26.III.1992, leg. Frisch (MNHUB); 1 ex., Corfu, leg. Hummler (MHNG).

Turkey: Tokat: 6 exs., Tokat – Almus, 1200 m, 21.V.1967, leg. Besuchet (MHNG). **Adana:** 2 exs., Kozan, 600 m, 5.V.1967, leg. Besuchet (MHNG); 1 ex., Kozan, 300 m, 5.V.1967, leg. Besuchet (MHNG). **Konya:** 1 ex., Çamlık env., Toroslar mts., 1345-1380 m, 6.-8.VI.2003, leg. Smatana (cSch). **Adiyaman:** 1 ex., Gölbaşi, 900 m, 10.V.1967, leg. Besuchet (MHNG).

Ukraine: 1 ex., Odessa (NHMW).

Locality not specified or illegible: 10 exs. (MHNG).

Diagnosis: See ASSING (2004a).

Distribution and bionomics: *Medon fusculus* is a widespread Ponto-Mediterranean element (Map 11), its distribution ranging from the Middle East, eastern Anatolia, West Caucasus, and Ukraine in the southeast and east to the southwest of France, southern England, and southern Norway, southern Sweden, and Lithuania in the west, northwest, and north (material examined; ASSING 2004a). For a selection of additional records see BOHÁČ (1985), BRUGE et al. (2001), DRUGMAND (1989), FOWLER (1888), HORION (1965), HUGENTHOBLER (1966), KOCH (1968), KÖHLER (2000), KÖHLER & KLAUSNITZER (1998), LINKE (1907), SCHOLZE & JUNG (1993), SILFVERBERG (1992), SZUJECKI (1968), TERLUTTER (1995), and UHLIG & VOGEL (1981). On the whole, *M. fusculus* is much more common in the southeast of its range (Turkey, Greece) than in the northwest, where it is rather rare. In France, it is absent from the Pyrénées-Orientales (TRONQUET 2001). In the British Isles, it is local and confined to the southern parts of England (FOWLER 1888). According to HANSEN (1996), it is absent from Denmark. In Sweden, it is known only from Södermanland (LUNDBERG 1995), but this record is somewhat doubful (M. SÖRENSSON, Lund, pers. comm. 2003). OUTERELO (1980) reports a record from southern Spain (Andalucía), adding that the species is known from Spain and Portugal. As can be inferred from the general distribution and the abundant *Medon* material examined from the Iberian Peninsula, however, *M. fusculus* is absent from the Iberian Peninsula and these records are most likely to be based on misidentifications (probably confusion with *M. ripicola*). *Medon fusculus* has been reported from various regions in Italy, including Sardinia and Sicily (CICERONI & ZANETTI 1995; HORION 1965; LUIGIONI 1929; PORTA 1926), but the results of the present revision suggest that all the records, except for those from the northeast (Friuli-Venezia Giulia), are probably erroneous.

Medon fusculus has been collected from various kinds of substrates, especially leaf litter, nests of mammals (mole, fox, vole, rabbit), compost, hollow trees, and flood debris in forests, gardens, gravel pits, river banks, etc. (ASSING 2004a; BOHÁČ 1985; FRANZ 1938; HORION 1933, 1965; WAGNER 2002; ZERCHE 1980). Many records are from mole nests; OSELLA & ZANETTI (1974) repeatedly found the species in this habitat, partly in larger numbers. On the other hand, STROUHAL & BEIER (1918) found only six specimens in 118 nests examined. According to NOWOSAD (2000) only very few specimens were collected in a total of 7000 nests studied in Poland; NOWOSAD (1990) had not found more than two specimens in 5000 mole nests dug up all over Poland. MEYBOHM (1997) reports two flight records (car-net); on one occasion 15 flying specimens were collected.

Adult beetles have been collected throughout the year. DRUGMAND (1989) states that the species is bivoltine, but there is no evidence supporting this. Based on the material examined here, *M. fusculus* is univoltine. According to BOHÁČ (1985), teneral specimens were observed in March.

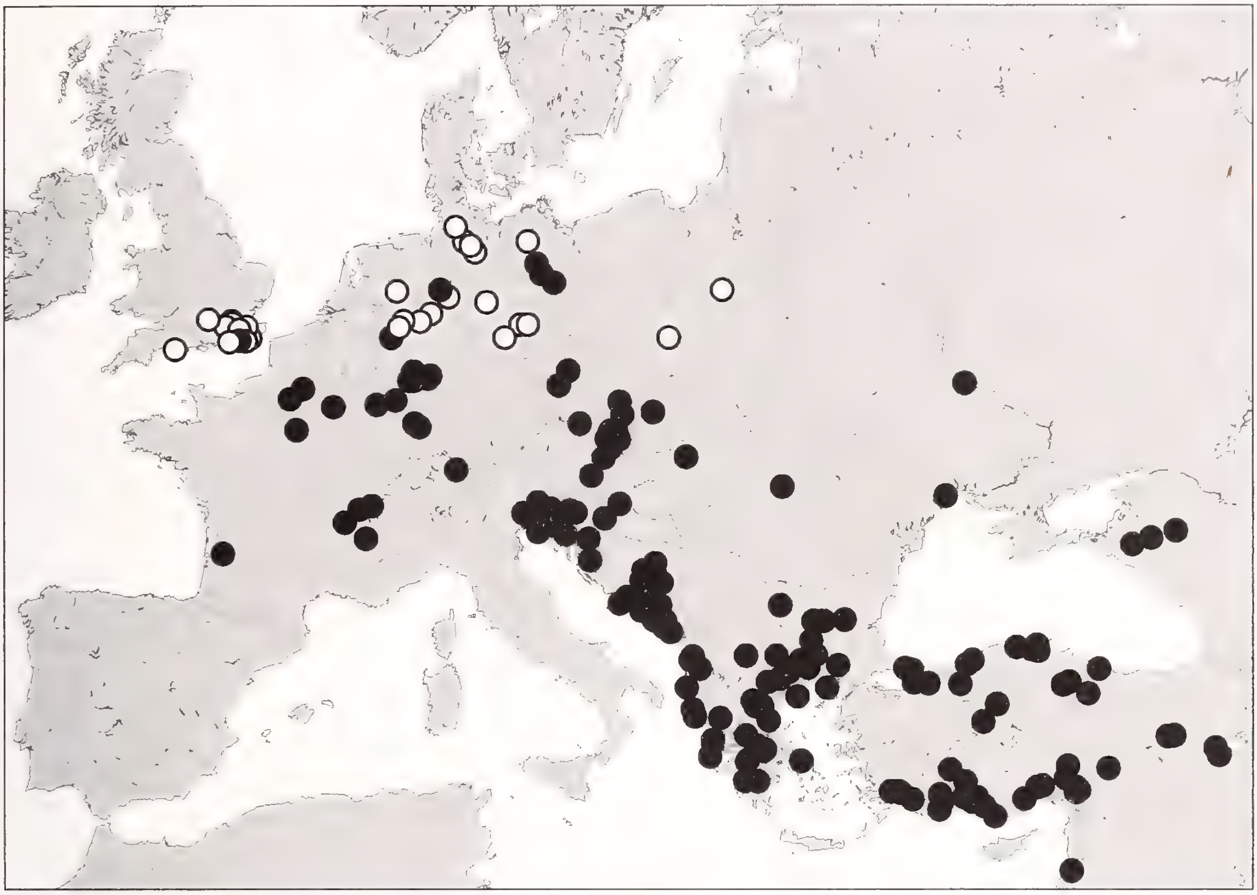
In the male seen from England, the male sternite VII and the aedeagus were teratologically malformed.

3.21. *Medon sardous* Dodero, 1922 (Figs. 95-99)

Medon sardous Dodero, 1922 (DODERO 1922: 67f).

Material examined (total: 18 exs.):

Italy, Sardegna: 6 exs., NNW Villaputzu, Salto di Quirra, 400 m, 9.X.1989, leg. Wunderle (cWun, cAss); 3 exs., grotta S. Puddu near Villaputzu, 17.VIII.1973 (cBor); 6 exs., Flumini (NHMW, cAss); 1 ex., Lanusei (NU), 12.V.1980, leg. Torchia (cZan); 1 ex., NW Lanusei (NU), 650 m, 21.IV.1992, leg. Schawaller (SMNS); 1 ex., N Domusdemaria, 38°58N, 8°52E, 23.X.1981, leg. Malicky (cAss).



Map 11: Distribution of *Medon fusculus* (Mannerheim) (filled circles: revised records; open circles: selected literature records).

Diagnosis: In external appearance similar to *M. fusculus*. 4.5-5.5 mm. Coloration reddish brown to dark brown, with the head usually slightly darker; legs and antennae yellowish brown to ferrugineous.

Head about as wide as long or weakly transverse and 1.10-1.15 times as wide as pronotum (Fig. 95); eyes relatively large, in dorsal view more than half the length of temples; puncturation dense, coarse, well-defined, and areolate; interstices with noticeable shine.

Pronotum approximately as wide as long or weakly transverse (Fig. 95); puncturation on the whole similar to that of head, but usually shallower, slightly less dense, and less well-defined; usually with, more rarely without impunctate median line.

Elytra relatively large, 1.20-1.25 times as wide and at suture about 1.1 times as long as pronotum (Fig. 95); puncturation much finer and less dense than that of head and pronotum; interstices shining. Hind wings apparently fully developed. Protarsomeres I - IV without sexual dimorphism, transverse in both sexes; tarsi relatively short, metatarsomeres III and IV less than twice as long as broad.

Abdomen finely and densely punctate; posterior margin of tergite VII with palisade fringe.

♂: posterior margin of sternite VII of similar morphology and chaetotaxy as in other species of the *M. fusculus* group, deeply and broadly concave (not distinctly trapezoid), with two lateral combs of palisade setae and on either side of middle with a distinct tuft composed of very long dark setae (Fig. 96); sternite VIII similar to that of *M. fusculus* and related species (Fig. 97); aedeagus of distinctive shape (Figs. 98-99).

Systematics and comparative notes: Based on external similarities (relatively large size, puncturation of head and pronotum), the male secondary sexual characters, especially the characteristic shape and chaetotaxy of sternite VII, and on the morphology of the aedeagus, *M. sardous* doubtlessly belongs to the *M. fusculus* group. From all the species of this group, none of which occurs in Sardinia (but see notes on *M. ripicola* below), it is distinguished especially by the distinctive shape of the aedeagus. From *M. fusculus*, the only geographically close congener of the *fusculus* group, it is additionally distinguished by the more well-defined puncturation and more shining interstices of the head and pronotum, by the shorter tarsi (metatarsomeres III and IV in *M. fusculus* more than twice as long as broad), transverse protarsomeres I - IV, the concave (not trapezoid) posterior excavation of the male sternite VII, and by the much more distinct and longer tufts of setae at the posterior margin of the male sternite VII.

Distribution and bionomics: *Medon sardous* is endemic to Sardinia and – together with *M. fusculus*, *M. ripicola*, and *M. kabylicus* – one of the westernmost representatives of the *M. fusculus* group. Additional Sardinian localities are summarized by Bordoni (1981), all of them are in the southern half of the island. The species was sifted from leaf litter and found in caves.

3.22. *Medon ripicola* (Kraatz, 1854) (Fig. 100, Map 12)

Lithocharis ripicola Kraatz, 1854 (Kraatz 1854: 127).

Lithocharis kellneri Kraatz, 1875 (Kraatz 1875: 123).

Medon pectiniventris Donisthorpe, 1932 (Donisthorpe 1932: 252).

Types examined: See Assing (2004a).

Material examined (total: 379 exs.; for additional material see Assing (2004a))**:**

Tunisia: 2 exs., Aïn Draham (= Ayn ad Darahim; 36°47N, 8°42E), leg. Bodemeyer [1 paralectotype of *M. bodemeyeri* Bernhauer] (DEI, MHNG); 2 exs., Aïn Draham, IX.1944, leg. Demoflys (cTro); 2 exs., Aïn Draham, VIII.1945, leg. Demoflys (cTro).

Algeria: 2 exs., Grande Kabylie, Oued Sébaou, W Dellys, 20.V.1988, leg. Besuchet, Löbl & Burckhardt (MHNG, cAss).

Morocco: 3 exs., Salé, leg. Thery (NHMW); 2 exs., Haute Atlas, Oukaimeden, leg. Franz (cAss); 1 ex., Oued Sebou, IV.1961, leg. Comellini (MHNG).

Portugal: 2 exs., Coimbra (NHMW); 1 ex., Algarve, Praia de Faro, 37°02N, 07°59W, 5 m, laguna, 26.III.2002, leg. Meybohm (cAss); 1 ex., Algarve, Serra de Monchique, Portela Viuva, 20.II.1999, leg. Meybohm (cAss); 1 ex., Lagoa da Casa, 28.III.1986, leg. Winkelmann-Klöck (cSch). **Madeira:** 2 exs., above Seixal, Rib. do Seixal, 550m, bank of stream, 31.III.1996, leg. Lompe (cAss); 1 ex., locality not specified, leg. Franz (cAss). **Azores:** 6 exs., São Miguel, Lagoa do Congro, 27.VIII.2003 (cAss).

Spain: Cataluña: 1 ex., Seo de Urgel, leg. Franz (cAss); 5 exs., Seo de Urgel, Arfa, V.-VI.1962, leg. Fagel (IRSNB); 4 exs., Seo de Urgel, V.-VI.1962, leg. Fagel (IRSNB); 4 exs., Gerona, Figueres, 10.VII.1965, leg. Comellini (MHNG, cAss). **Galicia:** 1 ex., Lugo, Linares, 1000 m, 27.V.1996, leg. Starke (cAss); 1 ex., Orense, Manzaneda, VII.1956, leg. Gonzales (MHNG). **Asturias:** 1 ex., Playa de Concho de Artedo, 3 km W Cudillero, 43°34N, 06°11W, 14.VI.2000, leg. Wrase (cSch); 2 exs., W Puerto de Pajares, Puerto de la Cubilla – Sotiello, 500 - 1400 m, car-net, 8.VI.1991, leg. Wunderle (cWun); 4 exs., Covadonga, VI.1965, leg. Fagel (IRSNB); 2 exs., Cudillero, Conche de Ariedo, 43°34N, 6°11W, 14.VI.2000, leg. Starke (cFel). **Aragón:** 1 ex., Sierra de Albarracín, V.1953, leg. Comellini (cBor). **Andalucía:** 2 exs., Sierra Nevada (GR), Lanjaron, 400 - 600 m, 23.III.1994, leg. Assing, Wunderle (cAss, cWun); 8 exs., Lanjaron, 26.IV.-18.V.1961, leg. Fagel (IRSNB).

British Isles: Wales: 1 ex., Powys, Brecon, 26.VI.1994, leg. Owen (cOwe).

Sweden: 1 ex., Halland, Dagsås, 4.IX.1986, leg. Gillerfors (cGil).

France: Bourgogne: 2 exs., Côte d´Or, Montigny sur [illegible] (NHMW). **Nord-Pas-de-Calais:** 2 exs., Lille (DEI, NHMW). **Picardie:** 3 exs., Laigneville (Oise), 1.IV.1930, leg. Mequignon (MHNG); 1 ex., Laigneville, leg. Mequignon (MHNG); 3 exs., Laigneville, 12.IV.1926 (MHNG); 1 ex., Bailleval (Oise), 24.IV.1927 (MHNG). **Île-de-France:** 2 exs., Sucy-en-Brie, leg. Mequignon (MHNG); 1 ex., Sucy-en-Brie, leg. Mequignon (MHNG). **Aquitaine:** 1 ex., Arette, 29.III.1960, leg. Jeanne (cBor); 1 ex., Castets, 30.VI.1938, leg. Gaudin (UCBA); 1 ex., Gironde, Cambes (MHNG); 3 exs., Cambes, 11.III.1939, leg. Giraud (MHNG); 1 ex., Gironde, locality illegible (MHNG); 4 exs., Bordeaux, bank of Garonne, 16.III.1930, leg. Tempère (MHNG); 1 ex., Gironde, Taussat-les-Bains, 10.IX.1934, leg. Tempère (MHNG); 1 ex., Gironde, Cubzac-les-Ponts, 23.III.1935, leg. Tempère (MHNG); 1 ex., Gironde, Langoiran, 15.IV.1946, leg. Tempère (MHNG). **Midi-Pyrénées:** 2 exs., Hautes-Pyrénées, locality not specified, leg. Pandellé (NHMW, UCBA); 1 ex., locality illegible, 25.V.1943, leg. Giraud (MHNG). **Languedoc-Roussillon:** 1 ex., Molitg les Bains, 550 m, 2.IX.2001, leg. Tronquet (cTro); 1 ex., Molitg les Bains, 600 m, oak leaf litter, 10.IV.2002, leg. Tronquet (cTro).7 exs., Carcassonne (NHMW); 1 ex., Cevennes, Villefort, Bresis, 9.III.2002, leg. Aßmann (cAss). **Auvergne:** 1 ex., Cantal, Thiézac, 28.VIII.1947, leg. Tempère (MHNG). **Rhône-Alpes:** 1 ex., Savoie, Belmont-Tramonet (NHMW); 3 exs., Haute-Savoie, Vougy, 6.IV.1965, leg. Comellini (MHNG, cAss); 1 ex., Ain, Divonne-les-Bains (MHNG); 1 ex., Ardéche, Mauves, 18.III.1906 (cSch); 3 ex., Haute-Savoie, Malagny, 14.XII.1961, leg. Comellini (cAss). **Provence:** 1 ex., Var, Roquebrune sur Argens, leg. Demoflys (cTro); 1 ex., Var, Gapeau inundation [near La Garde], X.1958 (MHNG); 1 ex., Var, Hyères, X.1958 (MHNG); 1 ex., Var, Vésubie inundation [near Lantosque], VI.1957 (MHNG); 1 ex., same locality, VI.1958 (MHNG); 1 ex., same locality, XI.1947 (MHNG); 1 ex., same locality, IV.1956 (MHNG); 2 exs., Argens (Le Muy), II.1937 (MHNG); 1 ex., Var, Dardennes, II.1956 (MHNG); 1 ex., Var, E Vidauban, Aille inundation, I.1955 (MHNG); 2 exs., Var, Loup inundation (W Cagnes), leg. Ochs (MHNG); 8 exs., Loup inundation, III.1951 (MHNG); 1 ex., Nice, I.1960 (MHNG); 3 exs., Alpes Maritimes, St.-Vallier-de-Thiey, V.1975, leg. Toumayeff (MHNG); 1 ex. [teneral], same locality, X.1975, leg. Toumayeff (MHNG); 1 ex., Eyguières, leg. Perrot (MHNG). **Alsace:** 1 ex., Strasbourg, Rhine inundation, IX.1954 (MHNG). **Corse:** 1 ex., S Galeria, Col Palmarella, 5.VI.1987, leg. Tronquet (cTro); 2 exs., E Ajaccio, Gravone inundation, X.1960 (MHNG). **Locality illegible or ambiguous:** 1 ex., Vilue (?), leg. Falcoz (MHNG); 2 exs., Touxadons, Canarive (?), XII.1960 (MHNG); 1 ex., Cussac, VI.1913 (MHNG); 2 exs., IX.1903, leg. Mequignon (MHNG).

Germany: Nordrhein-Westfalen: 3 exs., Südlohn, chalk quarry, 21.IV.2001, leg. Scharf (cFel); 1 ex., Hürth, Tagebau Ville, 26.III.1989, leg. Köhler (cKöh); 3 exs., Wesseling, Berzdorf, Kiesgrube, 24.IV.1991, leg. Köhler (cKöh); 4 exs., Vadrup, Emsufer, Hof Schulte-Bisping, 25.V.1997, leg. Köhler (cKöh); 1 ex., Troisdorf, Kiesgrube Eschaar, 27.IV.1991, leg. Köhler (cKöh). **Hamburg:** 6 exs., locality not specified (NHMW). **Rheinland-Pfalz:** 2 exs., Eifel, Cochem, Bengel, 5.VI.1992, leg. Köhler (cKöh); 1 ex., Sinzig, 26.IV.1991, leg. Köhler (cKöh); 2 exs., Schaidt Bienwald, NWR Stuttpferch, 30.V.1996, leg. Köhler (cKöh); 1 ex., Wiltingen, car-net, 7.VI.1996, leg. Köhler (cKöh). **Bayern:** 1 ex., München, V.1930, leg. Pfaundler (MHNG). **Berlin/Brandenburg:** 1 ex., Eisenhüttenstadt, 9.IX.1980, leg. Pütz (cSch); 1 ex., Eisenhüttenstadt, 2.VII.1984, leg. Pütz (cSch); 13 exs., Sperenberg (DEI). **Thüringen:** 1 ex., locality not specified (NHMW). **Sachsen:** 1 ex., Klitten, 30.V.1978, leg. Vogel (cWun); 1 ex., Oberlausitz, Daubitz, flood debris, 23.IV.1994, leg. Schülke (cSch); 1 ex., Oberlausitz, Kreis Bautzen, Guttau, edge of pond, 26.V.1985, leg. Schülke (cSch); 2 exs., Guttau, car-net, 25.V.1985, leg. Schülke & Heinig (cSch); 2 exs., Guttau, 22.V.1983, leg. Schülke (cSch).

Switzerland: 1 ex., Morges (NHMW); 3 exs., shore of Lac de Neuchâtel, Vaumarcus, 26.VII.1992, leg. Zanetti (cZan); 1 ex., Bressigny (MHNG).

Austria: Vorarlberg: 5 exs., locality not specified, leg. Müller (NHMW); 1 ex., Lustenau/Lauterach, 400 m, flood debris, 13.V.1991, leg. Möseneder & Brandstetter (cSch). **Niederösterreich/Wien:** 2 exs., Wien (NHMW); 1 ex., Stockerau (NHMW); 1 ex., Klosternau (?), leg. Scheerpeltz (NHMW); 1 ex., Lobau, leg. Mandl (NHMW); 1 ex., Ysper, 16.IV.1992, leg. Peschel (cSch). **Steiermark:** 1 ex., Graz, leg. Strupi (NHMW).

Italy: Trentino-Alto Adige: 1 ex., Trento, Storo, 28.V.1977 (cAss); 5 exs., Adige ("Etsch-Au"), leg. Breit (NHMW). **Lombardia:** 2 exs., 10 km E Mantova, Barbassolo, IX.1976, leg. Carpacchia (cBor); 9 exs., Val Camonica, Cogno, leg. Krüger (NHMW, cAss); 1 ex., Solferino (MN), 24.X.1971, leg. Cormacchio (cZan); 1 ex., Sondrio, mole nest, 7.XI.1971, leg. Zanetti (cZan); 1 ex., Bergamo, Buco d. Corno, 9.VIII.1976, leg. Rossi (cZan); 1 ex., Ostiglia, Palude del Busatello, 12.III.1981, leg. Zanetti (cZan); 2 exs., Torbiere d'Iseo (BS), 28.III.1982, leg. Zanetti (cZan); 1 ex., Pozzolengo (BS), 15.IV.1984, leg. Zanetti (cZan); 1 ex., Mantova, Ponti sul Mincio, 27.I.1980, leg. Zanetti (cZan); 1 ex., Monte Marenzo (BG), 200m, 23.II.1997, leg. Tagliapietra & Zanetti (cZan); 5 exs., Pavia, bank of Ticino river, 3.XI.1958, leg. Rosa (UCBA); 2 exs., Cogno near Bienno, leg. Krüger (MHNG). **Piemonte:** 2 exs., Vercelli, 5.&12.IV.1964, leg. Olmi (cBor); 6 exs., Leini (TO), mole nest, 8.II.1966, leg. Osella (cBor); 5 exs., Leini, in *Salix* litter with *Lasius fuliginosus*, 25.IV.1964 (cZan); 14 exs., Leini, 20.-21.II.1965, leg. Osella (UCBA, cZan); 6 exs., Locana (TO), inundation, X.1960 (MHNG). **Liguria:** 4 exs., Altare, VIII.1968 & VII-IX.1974, leg. Bordoni (cBor, cTro); 1 ex., Arenzano (GE), 12.XI.1977, leg. Parodi (UCBA); 1 ex., same locality, 20.X.1969, leg. Briganti (UCBA); 1 ex., same locality, 15.II.1960, leg. Gardini (UCBA); 5 exs., NW Albenga, Leca, 15.IV.1973, leg. Briganti, Zoia (UCBA); 4 exs., Genova, 1920, leg. Mancini (UCBA). **Veneto:** 2 exs., NW Monselice, Colli Euganei (NHMW); 7 exs., NW Villafranca di Verona, Custoza, 22.I.1972, leg. Zanetti (cZan); 1 ex., Nogara (VR), Ponte Molino, V.1974, leg. Zanetti (cZan); 1 ex., Montecchia di C. (VR), mole nest, 22.II.1976, leg. Zanetti (cZan); 1 ex., Gazzo (VR), Palude del Busatello, caricetum, 12.III.1981, leg. Zanetti (cZan); 3 exs., Pellegrina (VR), mole nest, 3.II.1980 (cZan); 1 ex., Pellegrina, mole nest, 26.II.1999, leg. Zanetti (cZan); 1 ex., S Vicenza, Fimon, Lago di Fimon, 31.X.1982, leg. Zanetti (cZan); 1 ex., San Martino Buon Albergo (VR), Musella, Ferrazzetta, mole nest, 28.II.1991, leg. Zanetti (cZan); 1 ex., Cavaion Veronese (VR), Palude Canova, 13.III.1994, leg. Zanetti (cZan); 1 ex., Piombino Dese (PD), 20.III.1994, leg. Zanetti (cZan); 1 ex., Feltre (BL), Anzù, 240 m, mole nest, 11.I.1998, leg. Zanetti (cZan); 1 ex., Lovadina near Spresiano, VI.1939, leg. Burlini (MHNG). **Friuli-Venezia Giulia:** 13 ex., Tagliamento, Fella estuary, 46°22N, 13°07E, 250 m, 12.-13.IX.1998, leg. Schülke (cSch, cAss); 6 exs., bank of Tagliamento river near Codroigo, 45°57N, 12°55E, flood debris, 12.IX.1998, leg. Schülke (cSch, cAss); 5 exs. Venezia, Tagliamento, Foce fiume, 19.IV.1973 & 20.IV.1990, leg. Zanetti (cZan); 1 ex., bank of Isonzo river, SE Villesse, 45°51N, 13°27E, flood debris, 13.IX.1998, leg. Schülke (cSch); 1 ex., Frisanco (PN), 1.V.1990, leg. Zanetti (cZan). **Toscana:** 2 exs., "Toscana" (NHMW); 1 ex., Toscana, S Altopascio,Vallino di Macchia (PI), 16.IX.1995, leg. Bordoni (cBor); 1 ex., Mte. Argentario, macchia, 29.III.1921, leg. Moczarski & Scheerpeltz (NHMW). **Campania:** 2 ex., Capriati al Volturno, 21.VII.1975, leg. Rossi (cZan). **Basilicata:** 1 ex., Lagonegro, Rivello Fiume Noce, 40°03N, 15°46E, 250 m, 10.V.2002, leg. Wunderle (cWun); 1 ex., Episcopia (PZ), bank of Sinni, 500m, 22.VII.1993, leg. Zanetti (cZan). **Sicilia:** 1 ex., M. Iblei, Noto (SR), F. Manghisi, 25.VII.1994 (UCBA); 1 ex., M. Iblei, Noto, 25.VII.1993 (UCBA); 2 exs., Peloritani, F.ra di Floresta, Santa Venera del Bosco, Frascianida (ME), 450 m, 23.VI.1995, leg. Adorno (UCBA); 1 ex., M. Iblei, Isola Ardito (near Palazzolo) (SR), Valle d´Ánapo, 5.III.1997 (cAss). **Locality ambiguous:** 2 exs., Fiume, leg. Meyer (NHMW).

Czech Republic: 1 ex., Bohemia, Doudleby nad Orlicí, 1944, leg. Roubal (MHNG).

Polish or Czech territory: 1 ex., Cieszyn ("Teschen"), leg. Wanka (MHNG).

Croatia: 2 exs., Istria, Rabac Luka, 15.-17.V.1990, leg. Wrase (cSch).

Locality not indicated or illegible: 9 exs. (MHNG).

Diagnosis: See ASSING (2004a); habitus as in Fig. 100.

Distribution and bionomics: *Medon ripicola* is an expansive Atlanto-Mediterranean element (Map 12). Based on the revised material and reliable literature records, its distribution extends from the Azores, Madeira, Northwest Africa, and the Iberian Peninsula in the west to southern England and southern Scandinavia in the north and northwest, and to Poland, Romania, Croatia, Bulgaria, and Montenegro in the east and southeast (material examined; ASSING 2004a). It has also been recorded from Lithuania (SILFVERBERG 1992). In Scandinavia, it is known only from Halland (material examined), Malmö, and Öland in southern Sweden (BARANOWSKI 1982; LUNDBERG 1995), as well as from Denmark (HANSEN 1996; HANSEN et al. 1994; V. HANSEN 1964). For a selection of additional records see ALLEN (1969), BERNHAUER (1940), BOHÁČ (1985), BRUGE et al. (2001), DRUGMAND (1989), FOWLER (1888), GILLERFORS (1986), HORION (1965), HUGENTHOBLER (1966), KOCH (1968), KÖHLER & KLAUSNITZER (1998), LUNDBLAD (1958), NORMAND (1935), SCHILLER (1989), TERLUTTER (1995), VOGEL (1979), and WITTWER (1988). According to CICERONI & ZANETTI (1995), the species has been recorded from Sardinia, where the closely related endemic *M. sardous* occurs, but I have seen no material from there.

In the north of its range, *M. ripicola* was repeatedly found in coastal habitats (ALLEN 1969; BARANOWSKI 1982; HANSEN 1964; HORION 1965). Frequently, it was collected from flood debris (spring and winter) and in other habitats near or at the banks of rivers and streams (material examined; see also HORION (1965), KOCH (1968), and LINKE (1913)). In northern Italy, it is very common and abundant in mole nests, especially near rivers and streams; in this habitat it excludes *M. perniger*, which inhabits mole nests in drier places (OSELLA & ZANETTI 1974). In a very comprehensive study of mole nests in Poland, however, NOWOSAD (1990) did not find a single specimen of *M. ripicola*. On many occasions, the species was sifted from the leaf litter of various kinds of – mostly deciduous – forests and even of macchia. As can be inferred from the examined material with precise altitude specification, *M. ripicola* occurs at lower and intermediate elevations; none of these specimens was collected above 1000 m.

Adult beetles have been observed throughout the year (material examined), though most specimens were found in spring. Flying specimens were caught by car-net in May and June. One examined specimen collected in October was teneral. According to DRUGMAND (1989), the species is bivoltine, but there is no evidence supporting this. Based on the material examined here, it is univoltine. *Medon ripicola* is the host of the endoparasitic tylenchid nematode *Parasitylenchus medonis* Wachek (WACHEK 1955).

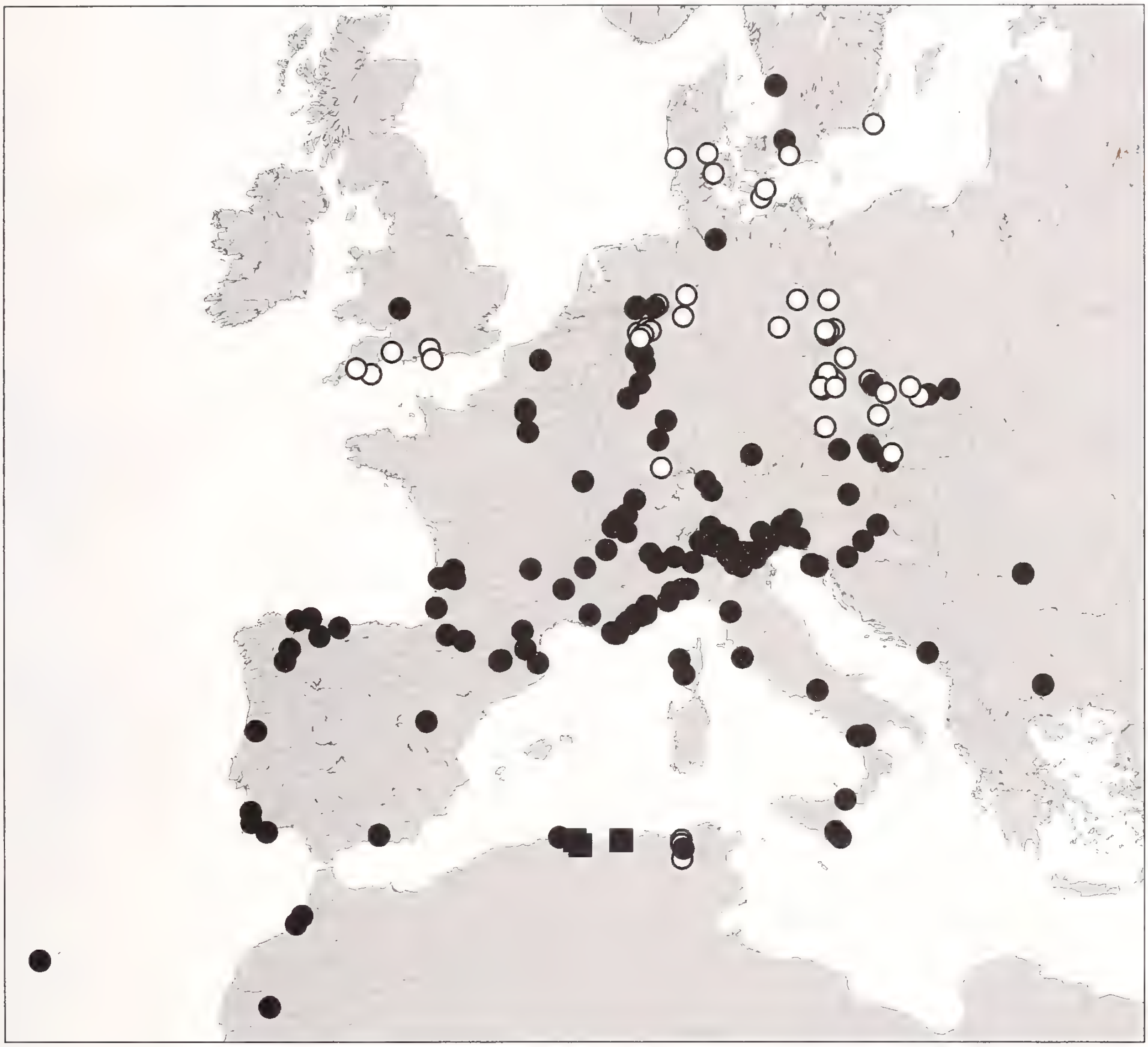
3.23. *Medon kabylicus* sp. n. (Figs. 101-105, Map 12)

Types: Holotype ♂: Gde Kabylie: Yakouren, forêt Beni-Ghobri, 800m, V.1953, G. Fagel / G. Fagel det., 1954, Medon ripicola / Holotypus ♂ *Medon kabylicus* sp. n. det. V. Assing 2003 (IRSNB). Paratypes: 2♂♂, 3♀♀: same data as holotype (IRSNB, cAss); 1♂, 3♀♀: Gde Kabylie: Yakouren, ravine au-dessus Tala Tegzirine, 860m, V.1953, G. Fagel (IRSNB); 5♀♀: Gde Kabylie: Yakouren, forêt Beni-Ghobri, Bois Sacré, 750m, V.1953, G. Fagel (IRSNB, cAss); 1♂: Gde Kabylie: forêt d´Akfadou, Tala Kitan, 1100m, 18V.1953, G. Fagel (cAss).

Description: 3.9-5.5 mm. Facies as in Fig. 101. Aside from the slightly wider protarsomeres I-IV (both sexes) and the male sexual characters, externally indistinguishable from *Medon ripicola*.

Usual coloration: head blackish brown to black, with the mouth parts lighter; pronotum and elytra rufous to yellowish, the elytra usually slightly lighter than the pronotum; abdomen reddish brown; legs and antennae rufous.

Head of subquadrate shape, approximately as wide as long; puncturation very dense, coarse, and areolate; surface almost without shine; interstices reduced to narrow ridges; eyes large, approximately 2/3 the length of postgenae in dorsal view.



Map 12: Distributions of *Medon ripicola* (Kraatz) (filled circles: revised records; open circles: selected literature records) and of *M. kabylicus* sp. n. (filled squares); the record of *M. ripicola* from the Azores is omitted.

Pronotum approximately as wide as long and at least slightly narrower than head; posteriorly weakly tapering; puncturation as in *M. ripicola* highly variable, ranging from fine and indistinct to relative coarse and well-defined.

Elytra distinctly wider than and at suture at least about 1.1 times as long as pronotum; puncturation very dense, slightly granulose, and not very well defined. Hind wings apparently fully developed. Protarsomeres I-IV slightly dilated in both sexes; protarsomere II distinctly transverse.

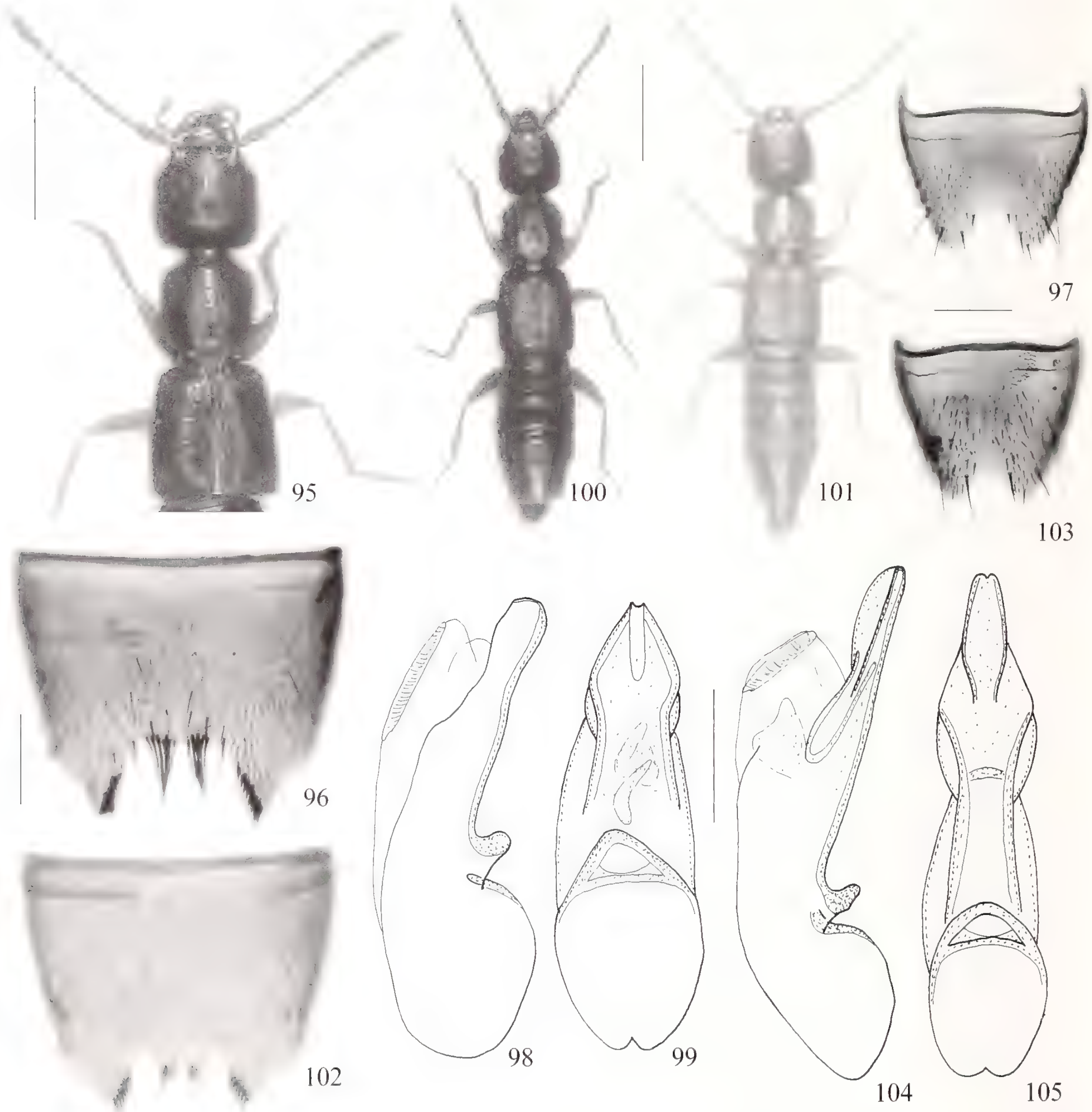
Abdomen with very fine and very dense puncturation; posterior margin of tergite VII with palisade fringe.

♂: posterior margin of sternite VII with broad trapezoid excavation (not shaped like a very wide V as in *M. ripicola*), with lateral combs of approximately 6 palisade setae and on either side of middle with tuft of several stout black setae (Fig. 102); sternite VIII similar to that of *M. ripicola* (Fig. 103); aedeagus very distinctive (Figs. 104 - 105), in lateral view apically wider and straight (in *M. ripicola* slightly bent dorsad) and in ventral apically shallowly incised, not deeply bifid as in *M. ripicola*.

Etymology: The name (adj.) is derived from the name of the Algerian mountain range, where the types were collected.

Comparative notes and systematics: *Medon kabylicus* and *M. ripicola* are doubtlessly adelphotaxa, as can be inferred from the synapomorphic highly derived morphology of the aedeagus. Both species can be distinguished only by the width of the protarsi (slightly dilated in *M. kabylicus*), by the morphology and chaetotaxy of the male sternite VII, and by the shape of the distinctive aedeagus.

Distribution and bionomics: *Medon kabylicus* is currently known only from Grande Kabylie, Algeria, where it apparently replaces *M. ripicola*. As far as is known today, both species seem to have an allo- or parapatric distribution (Map 12). Apart from the altitude (750-1100 m) and the fact that the types were collected in forests, no further bionomic data are available.



Figs. 95-105. *Medon sardous* Dodero (95-99), *M. ripicola* (Kraatz) (100), and *M. kabylicus* sp. n. (101-105): forebody (95); male sternite VII (96, 102); male sternite VIII (97, 103); aedeagus in lateral and in ventral view (98-99, 104-105); habitus (100, 101). Scale bars: 95, 100, 101: 1.0 mm; 96-99, 102-105: 0.2 mm.

3.24. *Medon indigena* (Wollaston, 1857)
(Figs. 106-110)

Lithocharis indigena Wollaston, 1857 (WOLLASTON 1857: 93).

Material examined (total: 133 exs.):

Madeira: Porto Santo: 11 exs., Pico do Castelo, 400m, mixed laurel and pine wood, 1.IV.1993, leg. Assing, Wunderle (cAss, cWun); 1 ex., Pico do Castelo, 300-430m, 11.IX.1998, leg. Schuh (cAss); 105 exs., Pico Juliana, 400m, mixed laurel and pine wood, 1.IV.1993, leg. Assing, Wunderle (cAss, cWun); 12 exs., same locality, 1.IV.1996, leg. Lompe, Zerche (DEI, cAss, cSch); 4 exs., Pico Facho, 500m, pine wood with scattered laurel trees, 1.IV.1996, leg. Assing (cAss).

Diagnosis: 4.2-5.0 mm. Habitus as in Fig. 106. Coloration variable, castaneous with blackish abdomen to blackish with slightly lighter elytra; legs light brown; antennae of variable coloration, light brown to dark brown, often with the central antennomeres slightly darker than the basal and apical ones.

Head weakly oblong, approximately 1.1 times as long as wide (Fig. 107); eyes small, less than half the length of postocular region in dorsal view and not projecting from lateral outline of head; puncturation distinct, relatively sparse, non-areolate, and rather fine; interstices on average wider than punctures; microsculpture usually absent from central dorsal area, visible only in posterior and lateral areas.

Pronotum approximately as wide as head or slightly narrower, weakly oblong; puncturation non-areolate, finer and denser than that of head, interstices narrower than punctures; microsculpture shallow, present at least in lateral areas of pronotum (Fig. 107).

Elytra small, only slightly wider than pronotum and at suture only approximately 0.8 times as long as pronotum; puncturation densely coriaceous; surface almost without shine (Fig. 107). Hind wings reduced.

Abdomen with very fine and dense puncturation, with distinct microsculpture, and with subdued shine; posterior margin of tergite VII without palisade fringe. Protarsomeres dilated in both sexes, with weak sexual dimorphism.

♂: protarsomeres I - IV slightly more dilated than in ♀; posterior margin of sternite VII very weakly concave, in the middle with fringe of weakly modified, long black setae (Fig. 108); sternite VIII posteriorly with deep emargination; aedeagus very distinctive (Figs. 109-110).

Comparative notes: This highly distinctive species is readily distinguished from its Western Palaearctic congeners by the sparse, fine, and non-areolate puncturation of the head, the reduced wings, the coriaceous elytra, and especially by the male sexual characters: the absence of palisade setae or distinctly modified setae at the almost truncate posterior margin of sternite VII, as well as the morphology of the aedeagus.

Comments: The types were not examined, but in view of the distinctive external morphology, sexual characters, and the restricted distribution, there are no doubts regarding the identity and interpretation of the species.

Based on the male primary and secondary sexual characters, *M. indigena* is most closely related to *M. feloi* Assing from the Canary Islands (see below). A closer relationship to the Madeiran endemic *M. vicentensis* Serrano, in contrast, is unlikely, based on the differences in the shape and chaetotaxy of the male sternite VII.

Distribution and bionomics: *Medon indigena* is endemic to the Madeiran archipelago and has been recorded from both Madeira proper and Porto Santo. While there are no recent records from the former, the species has repeatedly been found in Porto Santo in the past decade. Numerous specimens were sifted from leaf litter and rotting wood on the northern slopes of Pico Juliana, Pico do Castelo, and Pico Facho.

3.25. *Medon feloi* Assing, 1998 (Fig. 111)

Medon feloi Assing, 1998 (ASSING 1998: 143f).

Type examined: See ASSING (1998).

Diagnosis: For a more detailed description see ASSING (1998).

4.1 mm. Coloration of whole body uniformly ferrugineous. Head large (Fig. 111), weakly oblong; eyes reduced to minute rudiments, without ommatidia; puncturation fine and relatively sparse, interstices much wider than punctures; surface with pronounced microreticulation and almost matt.

Pronotum distinctly narrower than head; weakly, but noticeably oblong; puncturation very fine and sparse, barely noticeable; microreticulation pronounced (Fig. 111).

Elytra widest near posterior margin, anterior external angles almost obsolete; only slightly wider and at suture somewhat shorter than pronotum; puncturation more distinct and microsculpture much weaker than on head and pronotum; dorsal surface with distinct shine. Hind wings completely reduced.

Abdomen with moderately dense and very fine puncturation; posterior margin of tergite VII without palisade fringe.

♂: posterior margin of sternite VII of similar shape and chaetotaxy as in *M. indigena*; aedeagus as illustrated by ASSING (1998).

Comparative notes: This highly distinctive cave-dwelling species is readily distinguished from other Western Palaearctic congeners by the completely reduced eyes, the reduced pigmentation and wings, and by the male sexual characters. The latter are highly similar to those of *M. indigena*, its presumable sister species. The only other species with (almost) completely reduced eyes known from the Western Palaearctic region are *M. vicentensis* Serrano from Madeira and *M. antricola* from El Hierro.

Distribution and bionomics: *Medon feloi* is a true troglobite and endemic to La Palma, Canary Islands.

3.26. *Medon subterraneus* Coiffait, 1970

Medon subterraneum Coiffait, 1970a (COIFFAIT 1970a: 703f).

Comments: The holotype of this species, whose description is based on a single male from Ibiza without indication of the type depository, was looked for, but not found in the Coiffait collection and in the Zoological Museum in Barcelona. COIFFAIT (1970c) corrected the locality data, but failed to specify the whereabouts of the holotype. Until this specimen becomes available, an interpretation of the species must rely on the original description; additional material has not become known.

According to COIFFAIT (1970a), *M. subterraneus* is characterized especially by adaptive reductions resulting from a subterranean habitat and by the male sexual characters. The eyes are only one fourth the length of the postocular region, the hind wings are of reduced length, the abdominal tergite VII lacks a palisade fringe, and the posterior margin of the male sternite VII is shallowly concave and has a row of sparse, weakly modified marginal setae; the aedeagus is of similar general morphology as that of *M. dilutus*, *M. pocofer*, and related species.

4. KEY TO THE *MEDON* SPECIES OF THE WESTERN MEDITERRANEAN

In the key below, *M. subterraneus* (described from Spain: Ibiza) and *M. spelaeus* (southeastern Spain) are not accounted for, since no material has become available for study. *Medon augur* from Corsica is tentatively included in the key, although its male sexual characters are unknown. Based on external characters, this doubtful species is close to *M. rufiventris* and *M. dilutus*, so that even if it should prove to be a valid species, it can be expected to have similar male secondary sexual characters.

1. Eyes strongly to almost completely reduced, at most 1/5 the length of postocular region in dorsal view, without pigmentation or ommatidia. Atlantic Islands. 2

– Eyes at least 1/4 the length of postocular region, composed of at least some ommatidia. 4

2. Large species of at least 5 mm. Eye less strongly reduced, approximately 1/5 the length of temples in dorsal view; head distinctly oblong and posteriorly tapering. Legs and antennae very long and slender. ♂: posterior margin of sternite VII as in Fig. 42, with a tuft of long black setae on either side of middle; aedeagus as in Figs. 44-45. Endemic to El Hierro, Canary Islands; troglobite. .... ***M. antricola*** sp. n.

– Eyes reduced to minute rudiments. Smaller species. Sexual characters different. 3

3. Head about as wide as long (Fig. 71). Antennae long and slender; antennomere VII distinctly oblong (Fig. 72). Pronotum approximately as wide as long, distinctly tapering caudad, and with shallow, but rather well-defined and distinct puncturation (Fig. 71). Protarsomeres I - IV dilated in both sexes. Elytra shorter. Posterior margin of ♂ sternite VII distinctly concave and with two combs of palisade setae; aedeagus: SERRANO (1993). Madeira: São Vicente. .... ***M. vicentensis*** Serrano

– Head noticeably oblong (Fig. 111). Antennae shorter; antennomere VII not oblong. Pronotum distinctly oblong, weakly tapering caudad, and with extremely fine, barely noticeable puncturation (Fig. 111). Protarsomeres not distinctly dilated. Elytra longer. Posterior margin of ♂ sternite VII almost truncate, with two clusters of long black setae in the middle, but without palisade setae; aedeagus: ASSING (1998). Canary Islands: La Palma. .... ***M. feloi*** Assing

4. Posterior margin of ♂ sternite VII with more or less pronounced clusters of long black setae, but without combs of palisade setae. 5

– Posterior margin of ♂ sternite VII with two combs of palisade setae. 9

5. Head shining, with sparse, well-defined, non-areolate puncturation (Fig. 107). Elytra at suture distinctly shorter than pronotum (Fig. 107); hind wings reduced. Abdominal tergite VII without palisade fringe. ♂: posterior margin of sternite VII truncate to weakly concave, with a cluster of rather sparse black setae on either side of middle (Fig. 108); aedeagus broadly truncate apically (Figs. 109-110). Endemic to Madeira proper and Porto Santo. .... ***M. indigena*** (Wollaston)

– Head matt or nearly so due to very dense puncturation and/or pronounced microsculpture. Elytra at suture longer than pronotum; hind wings not reduced. Abdominal tergite VII with palisade fringe. ♂: posterior margin of sternite VII at least weakly bisinuate, with much more numerous black setae, and, in addition to lateral clusters, also with central cluster of black setae; aedeagus with bifid or with narrowly elongated apex (ventral view). The *M. apicalis* group. 6

6. Head with shallower and less coarse puncturation (Fig. 13). Puncturation of pronotum very fine, barely noticeable. Pronotum almost completely without shine due to pronounced microsculpture (Fig. 13). ♂: posterior margin of sternite VII with rather few and very slender black setae (Fig. 14); aedeagus with very long and slender ventral process of distinctive shape (Figs. 15-16). Canary Islands: Gran Canaria. . ... ***M. oromii*** sp. n.

– Head with coarser puncturation. Puncturation of pronotum fine and often shallow, but dense and distinct. Pronotum with at least subdued shine. ♂: posterior margin of sternite VII in the middle with more numerous and stouter black setae (e.g. Fig. 3); with much shorter and apically bifid ventral process. 7

7. Head on average with slightly more distinct puncturation (Fig. 1). ♂: posterior margin of sternite VII in the middle with distinct convex projection (i.e. distinctly bisinuate) and, especially in the middle, with darker, stouter, and longer modified setae (Figs. 2-3); aedeagus with ventral process of distinctive morphology: deeply bifid, apices widely separated, and subapically dentate (Figs. 5-7). Italy, southern Switzerland, southeastern France (Map 3). .... ***M. perniger*** Coiffait

– Puncturation of head usually ill-defined and confluent. ♂: posterior margin of sternite VII in the middle weakly convex (i.e. more weakly bisinuate) or concave, with shorter and more slender modified setae. 8

8. ♂: posterior margin of sternite VII in the middle weakly convex; aedeagus compact and apically bifid (ASSING 2004a, figs. 1-3). Widespread in the Western Palaearctic region, from the Atlantic Islands to Croatia and Bosnia-Herzegovina in the southeast (Map 2). .... ***M. apicalis*** (Kraatz)

– ♂: posterior margin of sternite VII in the middle weakly concave (Fig. 10); aedeagus with very long and apically acute ventral process (Figs. 11-12). N-Algeria, NW-Tunisia (Map 2) .... ***M. sericellus*** (Fairmaire)

9. Posterior margin of ♂ sternite VII with very deep and broad, trapezoid or concave emargination, with two combs of palisade setae, and, except for one species (*M. ripicola*), additionally with numerous long black setae on either side of the middle, usually grouped in more or less distinct tufts. Protarsi at most weakly dilated and without sexual dimorphism. Aedeagus either with apically truncate or with distinctly elongated ventral process of highly distinctive shape. Elytra distinctly wider and at suture longer than pronotum. The *M. fusculus* species group 10

– Posterior margin of ♂ sternite VII with shallower excavation and – except for one species from the Canary Islands – without (tufts of) long black setae on either side of the middle; sternite VIII usually with smaller emargination posteriorly. 13

10. Posterior margin of ♂ sternite VII with deep excavation of distinctly trapezoid shape and on either side of middle with long thin setae not arranged in distinct tufts. Aedeagus apically truncate (ASSING 2004a, figs. 66-71). Widespread species; distribution ranging from Great Britain to the Middle East, but absent from the southwestern Mediteranean (Map 11). .... ***M. fusculus*** (Mannerheim)

– Posterior excavation of ♂ sternite VII either shallower or not distinctly trapezoid, on either side of middle either without or with tufts of stout black setae. Aedeagus with apically distinctly elongated ventral process. 11

11. Larger and on average darker species (Fig. 95), forebody brown to dark brown; head only slightly darker than pronotum. Posterior margin of ♂ sternite VII as in Fig. 96. Aedeagus as in Figs. 98-99. Endemic to Sardinia. .... ***M. sardous*** Dodero

– Smaller and more distinctly bicoloured species, pronotum usually rufous and distinctly contrasting with the blackish or blackish brown head. ♂ sexual characters different. 12

12. Protarsomeres I-IV not dilated, protarsomere II approximately as wide as long; posterior margin of sternite VII in the middle obtusely angled, on either side of middle without tufts of stout black setae; aedeagus distinctive (ASSING 2004a, figs. 118-120), apically in ventral view narrowly and deeply incised. Widespread from NW-Africa, the Canary Islands and the Azores to southern Scandinavia, Lithuania, Poland, Bulgaria, and Montenegro (Map 12). .... ***M. ripicola*** (Kraatz)

– Protarsomeres I-IV slightly dilated, protarsomere II much wider than long; posterior margin of sternite VII with trapezoid excavation, in the middle truncate, on either side of middle with a tuft of stout black setae (Fig. 102); aedeagus distinctive (Figs. 104-105), apically in ventral view without narrow deep incision. Algeria (Map 12). ***M. kabylicus*** sp. n.

13. ♂: protarsi I-IV unmodified, in one species weakly dilated; aedeagus apically rounded, truncate, or with obtuse or rounded apico-lateral angles. 14

– ♂: protarsi I-IV more or less strongly dilated; aedeagus apically either incised or with the apical and the lateral margins meeting at an acute angle; ventral process not strongly elongated. 18

14. Eyes very small, about one fourth the length of temples in dorsal view (Fig. 90). ♂: aedeagus as in Figs. 92-94. Known only from one locality in northern Algeria. .... ***M. mirei*** Coiffait

– Eyes larger, more than one third the length of temples in dorsal view. Aedeagus different. More widespread species. 15

15. Head with finer puncturation (Figs. 74-75). Head and pronotum usually blackish. ♂: aedeagus as in Figs. 77-78. From the south of the Iberian Peninsula to southern England and Central Europe. Absent from NW-Africa, the Balkans, and apparently also from Austria and from central and southern Italy (Map 9). .... ***M. piceus*** (Kraatz)

– Head with very coarse puncturation. Head and pronotum usually (but not always!) rufous to dark brown. ♂: aedeagus of different shape. 16

16. Of larger average size and often with relatively larger head (though these characters are subject to considerable intraspecific variation). Elytra usually shorter, at suture approximately as long as pronotum. ♂: aedeagus larger (ASSING 2004a, figs. 40-41). From the Bosporus, Greece, and southern mainland Italy in the south and southeast to southern Scandinavia, southern England, western France in the north and west (Map 8). Distribution in the Iberian Peninsula limited to the northeast (Cataluña). ... . ***M. brunneus*** (Erichson)

– On average smaller and with relatively smaller head. Elytra at suture usually at least slightly longer than pronotum, only in brachypterous morph of *M. despectus* as long as pronotum. ♂: aedeagus smaller and of different shape. NW-Africa, Iberian Peninsula, and SW-France. 17

17. ♂: ventral process of aedeagus of trapezoid shape in ventral view (Figs. 82-84). Distribution: Morocco to SW-France. .... ***M. cauchoisi*** Jarrige

– ♂: ventral process of aedeagus apically rounded in ventral view (Figs. 88-89). Confirmed records only from Tunisia and Algeria. ***M. despectus*** (Fairmaire)

18. Head and pronotum with conspicuously coarse and well-defined puncturation; punctures of head areolate and very dense, interstices reduced to narrow ridges. Abdomen with rather sparse puncturation. ♂: aedeagus as figured by ASSING (2004a). Predominantly Eastern Mediterranean species, ranging from eastern Anatolia to southeastern Austria, the Czech Republic, and Slovakia. . ***M. ferrugineus*** (Erichson)

– Head and pronotum with finer puncturation; punctures of head not areolate. Abdomen with very dense and fine puncturation. ♂: aedeagus of different shape. 19

19. Very large species, body length usually >6.0 mm. Legs and antennae very slender; metatarsi almost as long as metatibiae. Sexual dimorphism of protarsi distinct, protarsomeres I - IV more strongly dilated in male than in female. ♂: aedeagus very long and slender. 20

– Smaller species, body length in normal preparation usually <6.0 mm. Legs and antennae not conspicuously long and slender; metatarsi much shorter than metabiae. ♂: aedeagus much shorter and less slender. 21

20. Largest species in the Western Palaearctic region, 7.0-9.0 mm (Fig. 53). Coloration uniformly ferrugineous. Head very large and of ellipsoid shape, lateral margins convex and posterior angles almost obsolete (Fig. 54). Length of metatibia 1.7 - 1.8 mm. ♂: sternite VII more oblong and posterior concavity shallower in relation to length of sternite (Fig. 55); aedeagus longer and with longer and more slender ventral process (Figs. 56-57). Known only from caves near Madrid. .... ***M. procerus*** (Perez Arcas)

– Usually smaller, 6.0-8.0 mm (Fig. 46). Head, most of pronotum, and anterior segments of abdomen blackish. Head of subquadrangular shape and with more distinct posterior angles (Fig. 47). Length of metatibia at most 1.4 mm. ♂: sternite VII less oblong and posterior concavity relatively deeper (Fig. 48); aedeagus shorter and with less slender ventral process (Fig. 49-52). Widespread from the south of the Iberian Peninsula to southern England, southern Scandinavia, and Central Europe (Map 6). .... ***M. castaneus*** (Gravenhorst)

21. Protarsomeres I - IV strongly dilated in both sexes (Fig. 59); meso- and metatarsomeres III and IV at least weakly transverse and almost cordiform. Head relatively large, weakly transverse, and somewhat flattened (Fig. 58). ♂: sternite VII and aedeagus as figured by ASSING (2004a). Confined to the coasts (under shingles and sea-weed) of western Europe, eastwards to Montenegro. .... ***M. pocofer*** (Peyron)

– Protarsomeres I - IV less strongly dilated; meso- and metatarsomeres III and IV oblong and not cordiform. Head not flattened. ♂: aedeagus of different shape. Species not usually occurring in coastal habitats. 22

22. Head distinctly oblong (Figs. 33-34); head and pronotum with pronounced microsculpture and very fine puncturation (Fig. 34). ♂: posterior margin of sternite VII with distinct tufts of long dark setae on either side of middle (Fig. 35); aedeagus as in Figs. 36-37. Endemic to Canary Islands. .... ***M. subcoriaceus*** (Wollaston)

– Head at most weakly oblong; head and pronotum usually with very shallow microsculpture and with coarser puncturation; exceptionally the microsculpture may be pronounced. ♂: posterior margin of sternite VII without distinct tufts of long dark setae on either side of middle; aedeagus of different shape. 23

23. Puncturation of head coarser, in dorso-median area sparser than in lateral areas. On average smaller species, 3.5 - 5.0 mm. 24

– Puncturation of head finer and evenly distributed, in dorso-median area as dense as in lateral areas. On average larger species, 4.0 - 6.0 mm. Aedeagus as in Figs. 24-28. 26

24. Large species of about 5.0 mm. Eyes smaller, weakly prominent and less than one third the length of postocular region in dorsal view (Fig. 73). Corsica. . ... ***M. augur*** Fauvel

– Smaller species of 3.5-4.5 mm. Eyes larger, distinctly projecting from lateral outline of head and about half the length of postocular region in dorsal view. 25

25. Head on average more transverse and often slightly dilated posteriorly. ♂: aedeagus with apical incision (ASSING 2004a, figs. 57-58). Widespread, from Caucasus region and Anatolia to Spain; confirmed records from NW Africa absent (Map 7). .... ***M. rufiventris*** (Nordmann)

– Head on average less transverse and usually not dilated posteriorly (Figs. 62-65). ♂: aedeagus without apical incision (Figs. 67-69). Known only from Tunisia and Algeria (Map 7). .... ***M. africanus*** (Fauvel)

26. Coloration of body more or less uniformly rufous to ferrugineous. Eyes slightly smaller. Elytra at suture approximately as long as pronotum (Figs. 17-21, 25-26). Unknown from North Africa and the Atlantic Islands. 27

– Head, usually at least the central part of the pronotum, and abdominal segments III - VII blackish. Eyes slightly larger and more prominent. Elytra at suture distinctly longer than pronotum (Figs. 30-32). Azores, Canary Islands, NW-Africa, Sicily (Maps 4, 5). .... ***M. dilutus quadriceps*** (Wollaston)

27. ♂: apex of aedeagus (ventral view) with subparallel lateral margins, pronounced apico-lateral angles, and with small median incision (Figs. 27-29). Southern mainland Italy and Central Europe. Unconfirmed records also from southern Scandinavia (Maps 4, 5). .. .. ***M. dilutus dilutus*** (Erichson)

– ♂: apex of aedeagus (ventral view) with convex lateral margins, indistinct apico-lateral angles, and with large median incision (Figs. 22-23). Southwestern Europe, Sardinia, southern England (Maps 4, 5). .... ***M. dilutus cephalus*** Koch

5. THE *MEDON* SPECIES OF THE EASTERN MEDITERRANEAN AND ADJACENT REGIONS: ADDENDA

Below, the material that has become available since the submission of the first part of the revision is listed. The records are commented on only when they are outside the known range of the species (see ASSING 2004a, 2004b).

***Medon maronitus* (Saulcy, 1864)**

Additional material examined:

Macedonia: 6 exs., Vardar plain, leg. Schatzmayr (NHMW, cAss). **Israel:** 12 exs., Galilee, Safad, 500 m, 30.V.1973, leg. Löbl (MHNG, cAss); 5 exs., Galilee, Mt. Meron, 900 m, 27.V.1973, leg. Löbl (MHNG, cAss). **Azerbaijan:** 2 exs., Talysh mts., road Lenkoran-.Lerik km 14-18, 30.IV.-9.V.2001, leg. Lackner (cAss); 1 ex., Talysh mts., Masalli – Isti Su, 10.-13.V.2001, leg. Lackner (cAss).

***Medon bucharicus* Bernhauer, 1902** (Figs. 112-116)

Medon bucharicus Bernhauer, 1902 (BERNHAUER 1902: 244).

Types examined: Lectotype ♂, present designation: ♂ / Buchara Staudinger / bucharicus Brh. Centralasien Type / Dr. M. Bernhauer donavit 29.IV.1942 / ex coll. Scheerpeltz / Typus Medon bucharicus Dr. Bernhauer / Lectotypus Medon bucharicus Bernhauer desig. V. Assing 2003 (NHMW). Paralectotypes: 1♂: same data as lectotype (NHMW); 1♂: same data, but "♀ / ... / Cotypus Medon bucharicus ..." (NHMW).

Additional material examined:

Tajikistan: 2 exs., Pamir Alai, Hissar Mts., Adshukcleft near Warsob, 1200 m, 1.-3.VII.1990, Schülke & Wrase (cSch); 1 ex., Hissar Mts., Warsob Valley, Siddi, 2000 m, 29.VI.1990, leg. Schülke & Wrase (cAss);

1 ex., Seravshan Mts., locality illegible, 1. VI. 1984, leg. Michailov (cSch). **Kirghizia:** 7 exs., Ferganskiy Alatau, Yarodar, 1400-1500 m, 16.-19.V.1993, leg. Schawaller (SMNS, cAss).

Comments: The original description is based on an unspecified number of syntypes. In order to secure the present interpretation of the species, one of the syntypes in the collections of the NHMW is here designated as lectotype.

Medon bucharicus was previously attributed to *Hypomedon* e.g. by COIFFAIT (1984), who, on p. 15 of the same work, however, mentions the same species as *Medon* in a footnote. As can be inferred especially from the morphology of the male sexual characters, the species doubtlessly belongs to the *Medon apicalis* group.

Diagnosis: 3.6-4.4 mm. Habitus as in Fig. 112. Head and pronotum castaneous to dark brown, head sometimes slightly darker than pronotum; elytra rufous to brown; abdomen brown to dark brown with lighter apex; legs and antennae rufous to brown.

Coloration somewhat variable; usual coloration: castaneous to blackish brown, with the head usually slightly darker than pronotum and elytra; legs and antennae testaceous yellowish brown, with the basal antennomeres usually reddish brown to ferrugineous.

Head 1.10 – 1.15 times as long as wide (Fig. 113); eyes of variable size, slightly more than half the length of postocular region in dorsal view, or much smaller, ca. one third the length of postocular region; integument with distinct microreticulation and with moderately dense, relatively shallow, but relatively large punctures. Antennae slender, preapical antennomeres only indistinctly transverse.

Pronotum weakly oblong, approximately as wide as head; microsculpture similar to that of head, but punctuation much finer, sparser, shallower, and ill-defined (Fig. 113).

Elytra at suture slightly longer (large-eyed specimens) (Fig. 112) or shorter (small-eyed specimens) than pronotum; puncturation dense and somewhat granulose; microsculpture indistinct, surface with much more shine than head and pronotum.

Legs relatively slender; metatarsi rather long, all tarsomeres much longer than wide, second tarsomere about 2.5 - 3.0 times as long as wide.

Abdomen with fine and moderately dense puncturation and with pronounced microsculpture; posterior margin of tergite VII with palisade fringe.

♂: posterior margin of sternite VII broadly and shallowly concave, and with cluster of modified black setae (Fig. 114); sternite VIII posteriorly broadly and deeply excavate; aedeagus of similar morphology as in *M. maronitus*, but larger, broader (ventral view), and in lateral view apically more distinctly dentate (Figs. 115-116).

Comparative notes: *Medon bucharicus* is somewhat similar to *M. maronitus*, but distinguished by larger body size, more uniform coloration of head and pronotum (in *M. maronitus*, the head is usually much darker than the pronotum), less dense puncturation of the head, clearly longer antennae, a much more strongly microsculpured and less densely punctured pronotum, relatively shorter elytra, longer tarsi (in *M. maronitus* the second metatarsomere is less than twice as long as wide), a different shape and chaetotaxy of the male sternite VII, a much deeper posterior emargination of the male sternite VIII, and a larger and broader aedeagus.

From *M. perniger* and *M. apicalis*, *M. bucharicus* is readily distinguished by less dense and less coarse punctuation of the head, by more pronounced microsculpture of the pronotum, by relatively smaller elytra, shorter metatarsi, and by different male sexual characters.

Intraspecific variation: Apparently, there are two morphs: the type specimens from Uzbekistan have relatively large eyes (more than half the length of postocular region in dorsal view) and longer elytra (Figs. 112-113), whereas the material seen from Tajikistan has small and weakly prominent eyes (about one third of the length of postocular region) and shorter elytra. However, the male primary and secondary sexual characters are essentially the same, so that the observed differences are attributed to intra- rather then interspecific variation.

Distribution and bionomics: *Medon bucharicus* has become known only from Tajikistan, Khirghizia, and Uzbekistan in Middle Asia. The specimens examined were collected at altitudes of 1200-2000 m during the period from May through July.

Medon cerrutii Coiffait, 1976

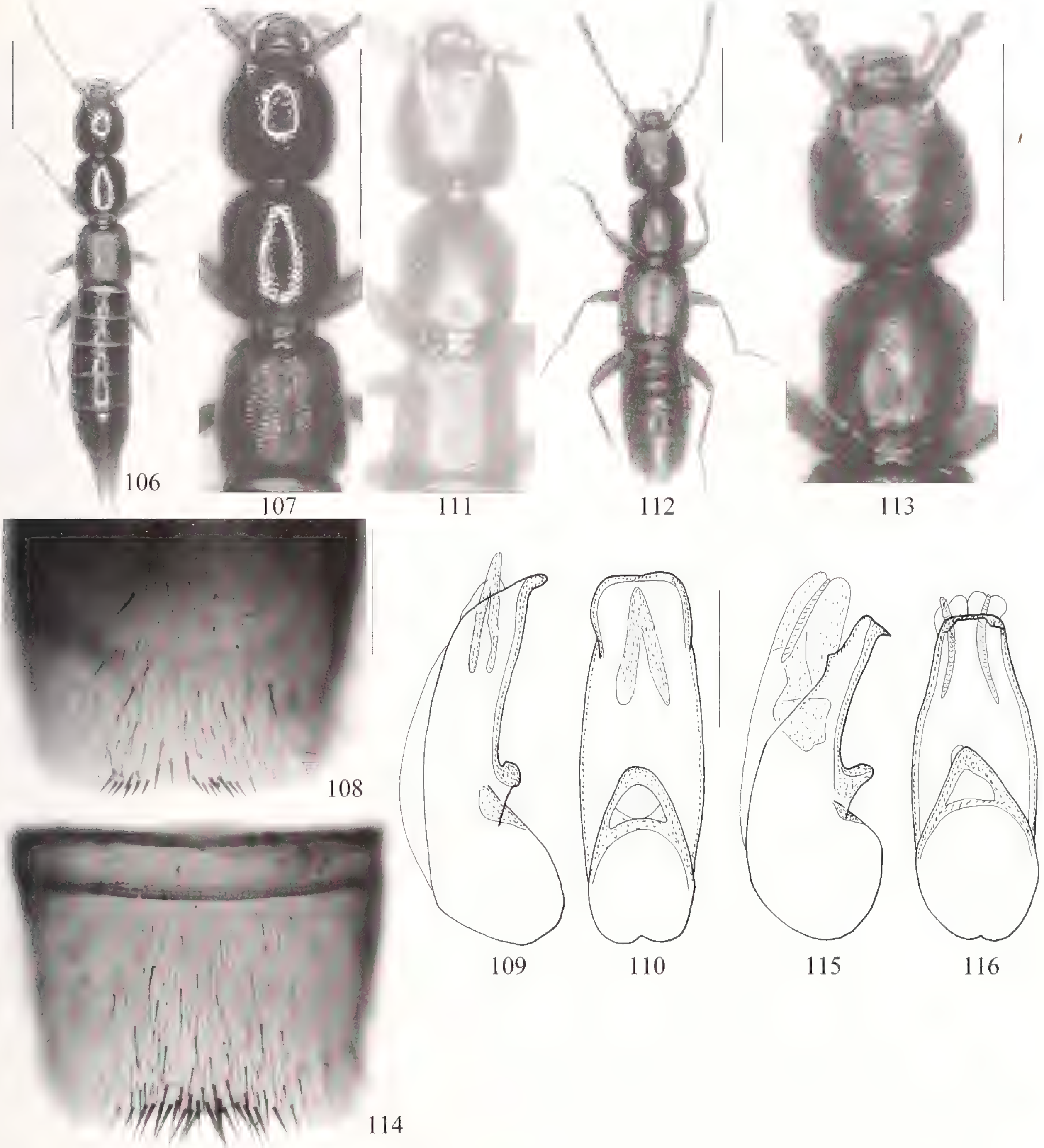
Additional material examined:

Crete: 6 exs., Zakros, 28.III.1973, leg. Meybohm & Fülscher (MHNG); 1 ex., Zakros, 20.III.1975, leg. Meybohm & Fülscher (MHNG).

Medon subquadratus Assing, 2004

Additional material examined:

Turkey: Adana: 2 exs., Kozan, 300 m, 5.V.1967, leg. Besuchet (MHNG, cAss).



Figs. 106-116. *Medon indigena* (Wollaston) (106-110), *M. feloi* Assing, holotype (111), and *M. bucharicus* Bernhauer (112-116; 112, 113: lectotype): habitus (106, 112); forebody (107, 111); male sternite VII (108, 114); aedeagus in lateral and in ventral view (109-110, 115-116); head and pronotum (113). Scale bars: 106-107, 111-113: 1.0 mm; 108-110, 114-116: 0.2 mm.

Medon guignoti Coiffait, 1987

Additional material examined:

Greece: 14 exs., Serrai, Hagiai Ioannis, wet moss, 17.VIII.1964, leg. Puthz (MHNG, cAss).

Medon semiobscurus (Fauvel, 1875)

Medon ruber Sahlberg, 1908 (SAHLBERG 1908: 33f) **syn. n.**

Medon sahlbergi Scheerpeltz, 1933 (SCHEERPELTZ 1933: 1255) [replacement name for *Medon ruber* Sahlberg] **syn. n.**

Types examined: *Medon ruber*: Lectotype ♂, here designated: Galilea / Vall. Kison / J. Sahlb. / Spec. typ. / 2410 / Mus. Zool. H:fors Spec. typ. No. 875 Medon ruber J. Sb. / Lectotypus *Medon ruber* Sahlberg desig. V. Assing 2003 / Medon semiobscurus (Fauvel) det. V. Assing 2003 (ZMH). Paralectotype ♀: same data as lectotype (ZMH).

Additional material examined:

Turkey: 14 exs., Muğla, Marmaris, V.1969, leg. Fagel (IRSNB); 4 exs., Antalya, Sugözü near Alanya, 15.III.2000, leg. Esser (cEss); 1 ex., Antalya, Akseki, 14.III.2000, leg. Esser (cEss); 1 ex., Antalya, Taşkesigi, 17.III.2000, leg. Esser (cEss); 1 ex., Antalya, Side, 13.III.2000, leg. Esser (cEss); 2 exs., Antalya, Killik, cave entrance, 780 m, 2.-4.VI.2003, leg. Lohaj (cSch); 11 exs., Kilik, 800 m, 3.VI.2003, leg. Smatana (cSch, cAss).

Syria: 1 ex., Caifa (?), leg. Simon (NHMW)

Israel: 1 ex., Carmel ridge, Dalya/Galed, 19./30.III.1995, leg. Sama (cZan); 3 exs., Mt. Carmel, Little Switzerland, 28.V.1973, leg. Löbl (MHNG).

Iran: 1 ex. [macropterous], Central Iran, Shapoor (NHMW).

Comments: The original description of *M. ruber* Sahlberg – a preoccupied name later replaced by *M. sahlbergi* Scheerpeltz, 1933 – is based on an unspecified number of syntypes. In order to secure the present interpretation of the name, the male syntype in the collections of the ZMH is here designated as the lectotype. The two type specimens belong to the short-winged, microsculptured and light-coloured morph of *M. semiobscurus* (see ASSING 2004a), so that *M. ruber* and its replacement name *M. sahlbergi* are synonymized with the senior name *M. semiobscurus* (Fauvel).

Distribution: *Medon semiobscurus* is here recorded from Syria and Iran for the first time.

***Medon dilutus pythonissa* (Saulcy, 1864)**

Medon pythonissa (Saulcy, 1864); ASSING (2004a).

Additional material examined:

Greece: Thrakia: 3 exs., Nomós Xánthi, Nestos near Toxótes, 25.IV.1994, leg. Schawaller (SMNS, cAss).

Turkey: 4 exs., Mersin, Tönük, 380m, 8.VII.1987, leg. Gardini, Rizzo, Zoia (cZan); 5 exs., Balikesir, Ayvalik, 15.VII.1969, leg. Besuchet (MHNG); 1 ex., Istanbul (NHMW); 2 exs., Antalya, Sugözü near Alanya, 15.III.2000, leg. Esser (cEss); 2 exs., Antalya, Güçlüköy near Akseki, 14.III.2000, leg. Esser (cEss); 3 exs., Antalya, Kilik, 800 m, 3.VI.2003, leg. Smatana (cSch, cAss).

Ukraine: 1 ex., Crimea, Jalta (NHMW); 2 exs., Odessa, Lusanwskij forest, rotting leaves, 22.X. 2003, leg. Gontarenko (cAss).

Jordan: 1 ex., Amman, 800 m, 25.III.1958, leg. Klapperich (MHNG).

Caucasus region: 1 ex., "Kaukas" (NHMW).

This taxon was previously referred to as *M. pythonissa* by ASSING (2004a), but is here regarded as a subspecies of *M. dilutus*. For further details see Section 3.5.

***Medon ferrugineus* (Erichson, 1837)**

Additional material examined:

Austria: 2 exs., Niederösterreich, Mistelbach, oak forest, 11.V.2002, leg. Zanetti (cZan); 3 exs., Bad Deutsch Altenburg, leg. Blühweiss (MHNG, cAss). **Locality not identified:** 3 exs., "Hackelsberg" (MHNG).

Slovakia: 1 ex., Štúrovo, VI.1963, leg. Rous (cBor); 3 exs., Kováčova, leg. Roubal (MHNG); 2 exs., Nitra, Zobor, 27.IX.1980, leg. Moravec (cKöh); 2 exs., Bratislava, Svatý jur, 220 m, 26.VI.1991, leg. Behne (DEI, cAss); 1 ex., Plášt´ovce, 14.IV.2000, leg. Hlaváč (cAss).

Romania: 1 ex., Comana Vlasca, leg. Montadon (MHNG); 2 exs., Cheile Turzli, 20.IV.1962, leg. Comellini (MHNG, cAss).

Bulgaria: 1 ex., Stara planina, VI.1968, leg. Rous (Bor).

Macedonia: 1 ex., Keretschkoi, leg. Schatzmayr (MHNG); 1 ex., Vardar plain, leg. Schatzmayr (MHNG).

Greece: 1 ex., Thessaloniki, leg. Schatzmayr (MHNG).

***Medon beroni* Coiffait, 1969**

Additional material examined:

Greece, Crete: 1 ex. [aedeagus teratological], W-Crete, Rethimnon, Dramia, bank of Mouselas river, IV.1997, leg. Feldmann (cFel).

***Medon lindbergi* Scheerpeltz, 1958**

Additional material examined:

Israel: 49 exs. [partly teneral], Mt. Carmel, Little Switzerland, 28.V.1973, leg. Löbl (MHNG, cAss); 9 exs., Galilee, below Safad, 500 m, 30.V.&14.VI.1973, leg. Löbl (MHNG, cAss); 1 ex., Galilee, Ginosar, 20.-21.V.1973, leg. Löbl (MHNG); 3 exs., 3 km E Ginosar, 24.V.1973, leg. Löbl (MHNG).

***Medon fusculoides* Coiffait, 1969**

Additional material examined:

Iran: 1 ex., Fars, Sivand, 30°07N, 52°58E, 10.VI.1974, leg. Senglet (MHNG); 1♀ [identification uncertain], Kohkiluyeh, Charam, 30°44N, 50°44E, 23.V.1974. leg. A. Senglet (MHNG).

***Medon lanugo* Assing, 2004**

Additional material examined:

Turkey: Antalya: 1 ex., ca. 30 km N Akseki, Bademli, Bademli geçidi, 2.-3.V.2001, leg. Lohaj (cAss). **Amasya:** 3 exs., Amasya-Ezinepazari, 22.V.1967, leg. Besuchet (MHNG).

The species was previously unknown from Amasya province (ASSING 2004a).

***Medon sparsiventris* Eppelsheim, 1889**

Additional material examined:

Azerbaijan: 2 exs., Masally, Istisu W Masally, 300 m, 18.-19.VI.1996, leg. Schawaller (SMNS).

6. THE *MEDON* SPECIES OF THE EASTERN MEDITERRANEAN AND ADJACENT REGIONS: CORRIGENDA

The recently published revision of the *Medon* species of the Eastern Mediterranean and adjacent region (ASSING 2004a) is unfortunately based on an early draft of the manuscript and not a revised version submitted to the editorial staff approximately one year prior to publication (18 June, 2003), in which the omission of a paper by COIFFAIT (1987) on two homonymies was corrected. In consequence, the revision contains a number of errors that require emendation. The following corrections (underlined) are proposed:

p. 33, abstract: ll. 5 f.: The previously unknown male sexual characters of *M. guignoti* Coiffait, 1987 are described. ll. 17 ff.: ... = *M. besucheti* Bordoni, 1980, **syn. n.**; *M. lydicus* Bordoni, 1980 = *M. mimulus* Fagel, 1970, **syn. n.**, = *M. rhodicus* Franz, 1987, **syn. n.** , = *M. choparti* Coiffait, 1987, **syn. n.**; *M. fusculoides* Coiffait, 1969 ...

p. 35, 3rd paragraph, ll. 1 ff.: Six species groups are present in the studied region: The *M. apicalis* group (3 species), the *M. petrochilosi* group (7 species), ...
same paragraph, ll. 17 ff.: *M. guignoti*, *M. petrochilosi*, *M. seleucus*, *M. cerrutii*, and *M. caricus*, which he referred to four different groups, are evidently closely related and here all included in the *M. petrochilosi* group, ...

p. 35, 5th paragraph, ll. 2 ff.: ... the Mediterranean region, the *M. petrochilosi* and the *M. fusculus* group are confined to the Eastern Mediterranean. The known distribution of the *M. petrochilosi* group ...

p. 35, 6th paragraph, ll. 8 ff.: ..., e. g. the majority of species of the *M. petrochilosi* group (*M. guignoti*, *M. cerrutii*, *M. seleucus*, *M. impar*, *M. subquadratus*).

p. 35, 7th paragraph, ll. 1 f.: The distribution patterns within the *M. apicalis* and the *M. petrochilosi* group, ...

p. 41, 3rd paragraph, ll. 5 f.: *M. cerrutii* is the sole representative of the *M. petrochilosi* group in Crete ...

p. 41: **3.6. *Medon guignoti* Coiffait, 1987 (Figs. 20-23, Map 4)**

Medon coriaceum Coiffait, 1969: 714f. (preoccupied).

Medon guignoti Coiffait, 1987: 497 (replacement name).

p. 42, legend to Figs. 20-23: *Medon guignoti* Coiffait: Aedeagus ...

p. 42, section 3.6, comparative notes, ll. 1 f.: From *M. cerrutii*, *M. petrochilosi*, *M. caricus*, and related species, *M. guignoti* is distinguished ...

p. 43, legend to Map 4: Distributions of *Medon petrochilosi* Coiffait (filled circles) and *M. guignoti* Coiffait (squares) in the Balkans, except for the type locality of *M. guignoti* based on revised records.

p. 44, Distribution and bionomics, ll. 5 ff.: ... but due to the external similarity of the species of the *petrochilosi* group, their identification is uncertain. ..., the species was found together with *M. lydicus*, *M. fusculus*, and *M. semiobscurus*.

p. 45, Comparative notes, ll. 1 ff.: *M. seleucus* is readily separated from *M. cerrutii*, *M. caricus*, *M. guignoti*, *M. petrochilosi*, and *M. impar* by the ...

p. 62, Distribution and bionomics, ll. 18 f.: ... the species was found together with *M. lydicus*, *M. caricus*, and *M. semiobscurus*.

p. 63: legend to Map 12: Distributions of *Medon beroni* Coiffait (squares), *M. subfusculus* Fagel (open circles), and *M. lydicus* Bordoni (filled circles) ...

p. 69, legend to Figs. 94-97: *Medon lydicus* Bordoni: Aedeagus ...

p. 69: **3.24. *Medon lydicus* Bordoni, 1980 (Figs. 94-97, Map 12)**

Medon lydicum Bordoni, 1980a: 114ff.

Medon umbilicatum Coiffait, 1970: 102ff.; **syn. n.** (preoccupied).

Medon mimulus Fagel, 1970: 157f. ; **syn. n.** (preoccupied)

Medon rhodicum Franz, 1987: 76ff.; **syn. n.**

Medon choparti Coiffait, 1987: 497; **syn. n.** (replacement name for *M. umbilicatus*).

p. 70, Comparative notes: *M. lydicus* is distinguished from other species of the *fusculus* group only by the ...

p. 70, Comments: delete last three paragraphs and replace with:

A comparison of the type material indicated above revealed that *M. umbilicatus* and *M. mimulus* are conspecific. The descriptions of both species were published in 1970; that of *M. umbilicatus* was published on June 30 (HERMAN 2001), whereas the date provided on the front cover of the issue containing the description of *M. mimulus* is September 15 (A. SMETANA, Ottawa, pers. comm. 2002). Both names are preoccupied, so that neither of them is eligible as the valid name of the species. *Medon umbilicatus* Coiffait is a primary junior homonym of *M. umbilicatus* Cameron, 1924 and *M. mimulus* Fagel is a secondary junior homonym of *Lithocharis mimulus* Casey, 1886, which is now in *Medon*.

Two species are represented in the type series of *M. lydicus*. The paratype belongs to *M. semiobscurus* (Fauvel); the holotype is conspecific with *M. umbilicatus* and the other names listed above. Since *M. lydicus* is the oldest unpreoccupied name, it is to be regarded as the valid name of the species. *Medon choparti* Coiffait is a replacement name for *M. umbilicatus* Coiffait and consequently a junior synonym of *M. lydicus* Bordoni.

An examination of the types of *M. rhodicus* Franz revealed that they are not specifically distinct from *M. umbilicatus*, so that *M. rhodicus* is here synonymized with the senior name *M. umbilicatus*.

p. 77, Key, couplet 3, ll. 8 f.: ... modified setae. The *M. petrochilosi* group.

p. 78, couplet 9, l. 10: ..... ***M. guignoti*** Coiffait

p. 80, couplet 30, l. 8: ..... ***M. lydicus*** Bordoni

p. 81, after Coiffait (1984) insert: COIFFAIT H. (1987): Nouvelles corrections homonymiques (Col. Staphylinidae). Nouvelle Revue d´Entomologie **3** (4) (1986): 497-498.

Acknowledgements. I am most grateful to all the colleagues indicated in the material section for the loan and/or gift of material under their care. In addition, my sincere thanks are due to the following colleagues for the communication of *Medon* records from England and Scandinavia: T. Clayhills (Parainen), E. Helve (Espoo), D. Lott (Birstall), I. Rutanen (Hyvinkää), and M. Sörensson (Lund). Benedikt Feldmann and Michael Schülke kindly proofread the manuscript.

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Received: 19.11.2003
Accepted: 15.04.2004
Revised: 07.01.2005

Corresponding editor: M. Schmitt

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Schneider, H. (2005): Bioakustik der Froschlurche – Einheimische und verwandte Arten. Mit Audio CD (beides zusammen erschienen als Supplement der Zeitschrift für Feldherpetologie 6). Laurenti Verlag, Bielefeld. 135 Seiten, 146 Abbildungen. ISBN 3-933066-23-9. Preis: 28,- €

Mit diesem kleinen Buch und der dazugehörigen CD legt der deutsche Nestor bioakustischer Forschung an Froschlurchen eine Zusammenfassung seiner langjährigen Forschungsarbeiten vor. Ausführlich dargestellt werden das Rufverhalten und die Rufe von Männchen und Weibchen von 25 Taxa aus verschiedenen Teilen Europas, aus dem Vorderen Orient und Kasachstan in Text und Abbildungen. Vorangestellt sind zwei kurze Einführungen, eine zu den Verhaltenszusammen-hängen, in denen Froschlurche Rufe äußern, und in die Terminologie dieser Rufe, die andere zur Bioakustik unter dem Titel „Akustische Merkmale der Paarungsrufe und Analyse der Rufe“. Die meisten Rufformen sind im Buch in paralleler Darstellung derselben Rufe im Oszillogramm (Zeitsignal) und Lautspektrogramm abgebildet. Der Text umfasst im wesentlichen die Beschreibungen der akustischen Strukturmerkmale der Rufe und geht für viele Taxa ausführlich auf deren Abhängigkeit von Luft- bzw. Wassertemperatur, bei der die Tiere rufen, sowie von ihrer Körpergröße ein. Die meisten Rufformen sind auf der CD mit Angabe der jeweiligen Temperatur, bei der diese aufgezeichnet wurden, mit Hörbeispielen dokumentiert.

Veröffentlichungen dieser Art wünscht man sich auch für weitere Tiergruppen, die zur Lautbildung befähigt sind, vor allen Dingen wie hier mit begleitender Audio-Dokumentation und so detaillierter Darstellung der verschiedenen Lautformen in Text und Analyse mit den dazugehörigen Abbildungen. So willkommen und nützlich diese Neuerscheinung ohne Zweifel ist, sie hat leider auch einige Aspekte, die man kritisch erwähnen muss.

Schnell fällt auf, dass eine nennenswerte Anzahl im Text zitierter Publikationen im Literaturverzeichnis fehlt (z.B. Blab 1982; Heinzmann 1970; Heusser 1969; Lörcher 1969; Lörcher & Schneider 1973; Müller 1984; Nascetti et al. 1996, 1999; Neubaur 1949; Radwan & Schneider 1988). Die online-Version der Weltliste „Amphibian Species of the World“ (Frost 2004) ist zwar zitiert, im Text des Buches wird aber bei Formen mit ‚wechselvoller' Taxonomie, zu der auch der Buchautor aktiv auf der Grundlage bioakustischer Befunde beigetragen hat, wie z. B. im Fall von *Rana balcanica*, darauf und den aktuellen Stand der Diskussion nicht Bezug genommen. Angaben über ihr Verbreitungsgebiet erfolgen nur für wenige Taxa. Nahezu alle abgebildeten Lautspektrogramme wurden mit relativ großem Zeitfenster und damit hoher Frequenz- und entsprechend geringer Zeitauflösung analysiert. Das führt angesichts der Tatsache, dass viele Rufe der untersuchten Froschlurche sehr schnelle Amplituden-Modulationen aufweisen, zu einer kaum angemessenen Darstellung der ‚eigentlichen' Rufstruktur in den Lautspektrogrammen. Dazu seien hier nur zwei Beispiele angeführt: Abb. 27 (Paarungsruf) und Abb. 28 (Befreiungsrufe) von *Bufo bufo* (S. 40). In beiden Fällen wird die in den Oszillogrammen gut sichtbare Struktureigenschaft einer schnellen Amplituden-Modulation in der ersten Hälfte der Rufe im Spektrogramm in der Frequenzdomäne dargestellt. Daher ist auch die Beschreibung der Struktur der letztgenannten Rufe im Text als „.... aus Impulsen bestehende erste Teil weist ein breites Spektrum auf, das bis 2500 Hz reicht und Frequenzbänder erkennen lässt, ...“ (S. 41) sachlich nicht wirklich zutreffend. Auch Unstimmigkeiten kommen vor. So wird in der Beschreibung der Struktureigenschaften der Paarungsrufe von Männchen und Weibchen der Geburtshelferkröte (S. 23 – 24, Abb. 12, 13) festgestellt, dass bei gleicher Körpergröße und Lufttemperatur die Grundfrequenz der Rufe (*der Weibchen?, G.P.*) um 60 – 80 Hz niedriger ist. Der in Abb. 12 gezeigte Paarungsruf eines Männchens (keine Größenangabe) bei 10 °C Lufttemperatur hat eine Grundfrequenz von um 1200 Hz, derjenige (Abb. 13) eines Weibchens (keine Größenangabe) bei 17 °C eine von um 700 Hz (Frequenzen jeweils aus dem abgebildeten Spektrogramm geschätzt). Die eigene lautspektrographische Analyse der beiden betreffenden Hörbeispiele auf der CD entspricht exakt den jeweiligen Abbildungen in dem Buch.

Trotz der genannten Kritikpunkte darf man abschließend festhalten, dass diese Neuerscheinung für interessierte Laien und Fachwissenschaftler eine Fülle interessanter Information bietet, die sie in vielfältiger Weise nutzen können. Angesichts des Buchtitels „Bioakustik der Froschlurche'' werden aber Leser mit spezifischen Erwartungen in dieser Hinsicht bioakustische Analysen und darauf fußende Beschreibungen der Lautstrukturen ‚lege artis' bei vielen Taxa vermissen.

G. Peters, Zoologisches Forschungsmuseum Alexander Koenig, Bonn

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SCOPOLI, I. A. 1763. Entomologia Carniolica. I. T. Trattner, Vienna.

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Bonner zoologische Beiträge

Herausgegeben vom

Zoologischen

Forschungsmuseum

Alexander Koenig,

Bonn

Band
54
Heft 3
2006 (2005)

Leibniz
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Bonner zoologische Beiträge werden publiziert im Eigenverlag Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn (Germany)

Die Zeitschrift erscheint mit vier Heften im Jahr, zum Preis von 11,50 € je Heft bzw. 46,- € je Band incl. Versand. Korrespondenz betreffend Abonnement, Kauf oder Tausch bitten wir zu richten an die Bibliothek, Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn (Germany). E-mail: d.steinebach.zfmk@uni-bonn.de.

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ISSN 0006-7172

Druck: Druck Center Meckenheim

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Bonner zoologische Beiträge	Band 54 (2005)	Heft 3	Seiten 97–102	Bonn, August 2006

A Revision of *Porocallus* Sharp. New Synonyms and New Species (Insecta: Coleoptera: Staphylinidae: Aleocharinae: Oxypodini)

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Abstract. A revision of types and additional material yielded the following synonymies: *Porocallus* Sharp, 1888 = *Platysmarthrusa* Pace, 1999 **syn. n.** = *Ischyradelia* Pace, 1999 **syn. n.**; *Porocallus insignis* Sharp, 1888 = *Platysmarthrusa chinensis* Pace, 1999 **syn. n.** Two new species are described and illustrated: *Porocallus hlavaci* **sp. n.** and *P. ligo* **sp. n.** *Porocallus tianmuensis* (Pace) **comb. n.** (previously in *Ischyradelia*) is briefly redescribed. New records of *P. insignis* from China and a key to the four species of the genus are presented. The distribution of the genus is mapped.

Key words. Eastern Palaearctic region - China, taxonomy, description, new records, distribution, key to species

1. INTRODUCTION

In a recent paper on the systematics of *Porocallus* Sharp, 1888 one species was recognized: the type species *P. insignis* Sharp, 1888 (ASSING 2001). The species is very widespread in the Eastern Palaearctic region, its distribution ranging from China to Japan. Based on additional material, which has become available in the meantime, and on a study of type material, three new synonymies are proposed and two new species are described. An additional undescribed species from Hubei is not named, as it is represented only by a single female; the external characters distinguishing it from other species of the genus are not pronounced and the spermatheca is not very distinctive.

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3. *POROCALLUS* SHARP, 1888

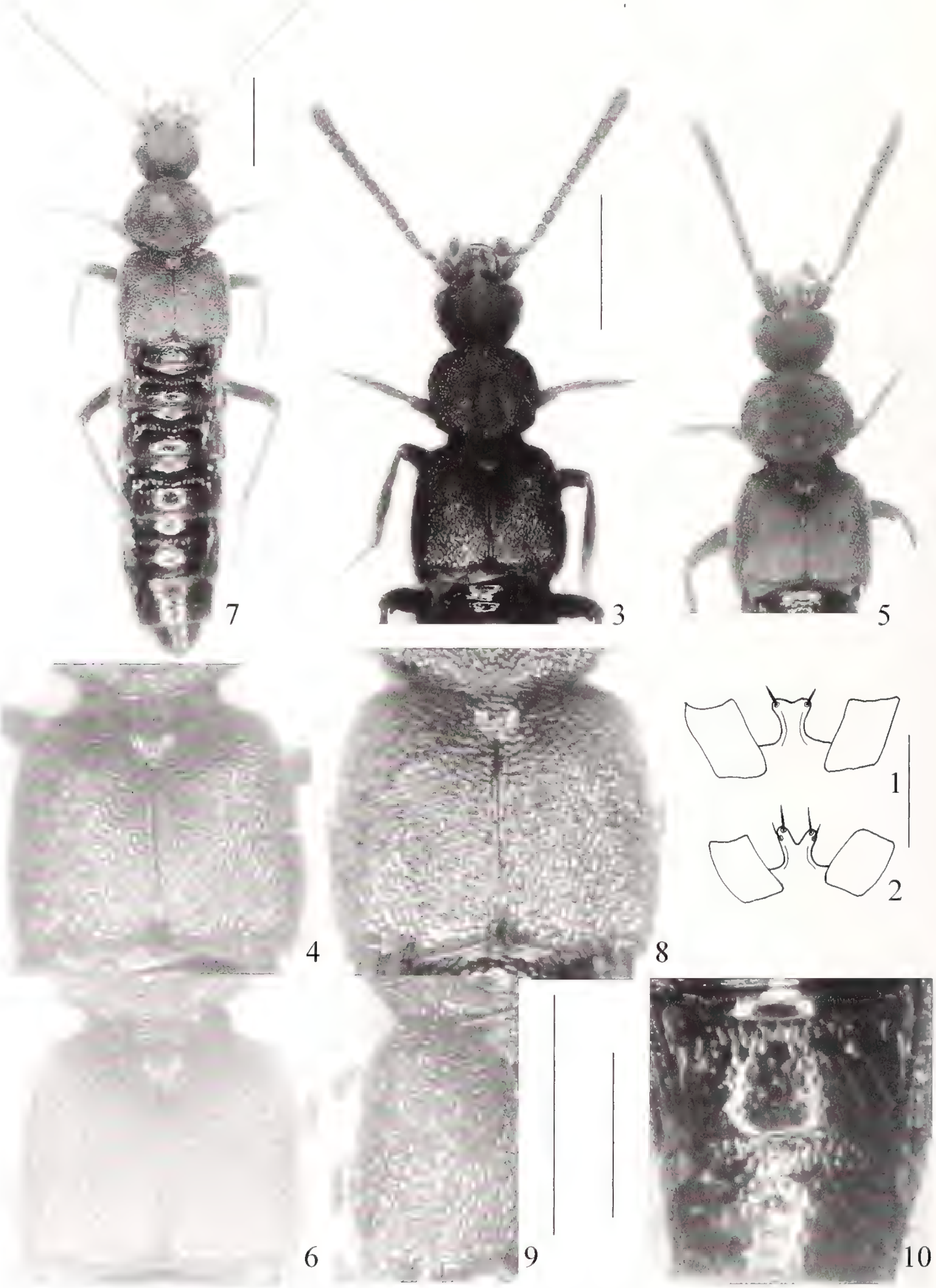
Porocallus Sharp, 1888 (SHARP 1888: 286f).

Platysmarthrusa Pace, 1999 (PACE 1999: 107f) **syn. n.**

Ischyradelia Pace, 1999 (PACE 1999: 108) **syn. n.**

Comments: When PACE (1999) described *Platysmarthrusa*, he did not compare it with *Porocallus*, a genus at that time known only from Japan. The type species of both genera are conspecific (see below), so that *Platysmarthrusa* is consequently a junior synonym of *Porocallus*. According to the original description of *Ischyradelia*, this taxon is distinguished from *Platysmathrusa* by the shape and chaetotaxy of the ligula, as well as by the stouter second joint of the maxillary palpus and the slightly larger first joint of the labial palpus.

An examination of the holotypes of both type species and of material of *P. insignis* from various localities revealed the following: The shape and chaetotaxy of the ligula are subject to considerable intraspecific variation (Figs. 1-2), so that differences seen in the ligulae of just two specimens do not justify a distinction at the generic level (in this case not even at the species level). The difference in the shape of the second joint of the maxillary palpus is clearly based on an artefact: in the holotype of the *Platysmathrusa chinensis*, it is much wider than illustrated by PACE (1999: 109); the impression of a slender joint is caused by the fact that it is turned on the slide, so that, when viewed from above, it is not seen at its widest aspect. Finally, the first joint of the labial palpus is in fact slightly less oblong, but this extent of variation is quite normal within genera; there are numerous examples of Staphylinidae with a much more pronounced intraspecific variation of the shape of the labial palpi. Most importantly, however, *Porocallus* is characterized by numerous highly conspicuous and very distinctive apomorphic characters states, all of them shared also by the holotype of *Ischyradelia tianmuensis*: especially the long, massive, and densely pubescent antennae, the conspicuous triangular flattened third joint of the maxillary palpi, the coarse and extremely dense puncturation of the forebody, and finally also the similar morphology of the primary and secondary sexual characters (see PACE 1999: 109-110). In addition, the facies is most similar (especially the shape of head and pronotum, the morphology of the abdomen), so that there is no doubt that *Ischyradelia tianmuensis* is in fact a species of *Porocallus* and that consequently *Ischyradelia* is a synonym of that name.



Figs. 1-10. *Porocallus insignis* Sharp (1-4), *P. hlavaci* sp. n. (5-6), *P. ligo* sp. n. (7-8), and *P. tianmuensis* (Pace) (9-10): ligulae of specimen from the Russian Far East (1) and of holotype of *Platysmarthrusa chinensis* Pace (2); forebody (3, 5); habitus (7); elytra (4, 6, 8, 9); abdominal segments VI and VII in dorsal view (10). Scale bars: 3-9: 1.0 mm; 10: 0.5 mm; 1-2: 0.08 mm.

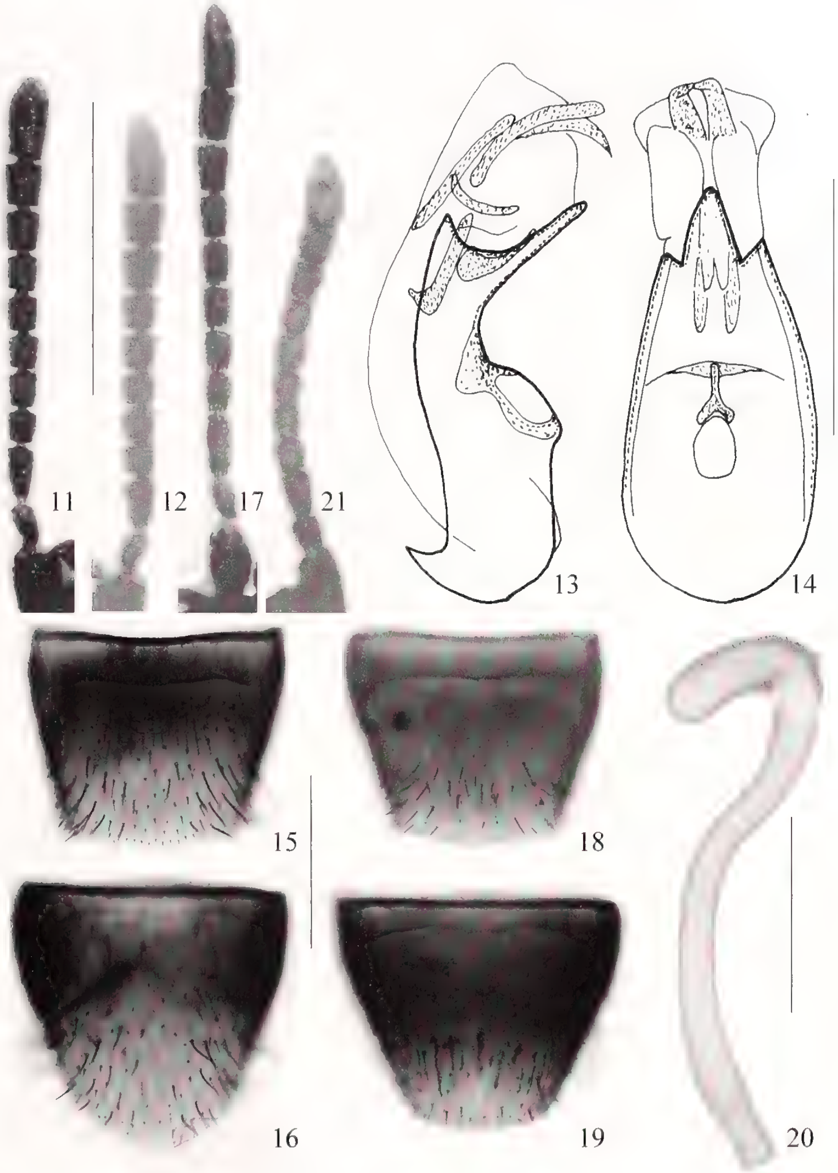
3.1. *Porocallus insignis* Sharp, 1888
(Figs. 1 - 4, 11, Map 1)

Porocallus insignis Sharp, 1888 (SHARP 1888: 287).

Platysmarthrusa chinensis Pace, 1999 (PACE 1999: 108) **syn. n.**

Types examined: *P. insignis*: see ASSING (2001).

P. chinensis: Holotype ♂: China Beijing, Songshan [ca. 80 km NW Beijing city centre], 15.V.1993, G. de Rougemont / Holotypus Platysmarthrusa chinensis m., det. R. Pace 1995 / Platysmarthrusa chinensis gen. n. sp. n. det. R. Pace 1995 / Porocallus insignis Sharp det. V. Assing 2003 (MHNG).



Figs. 11-21. *Porocallus insignis* Sharp (11), *P. hlavaci* sp. n. (12-16), *P. ligo* sp. n. (17-20), and *P. tianmuensis* (Pace) (21): antenna (11, 12, 17, 21); median lobe of aedeagus in lateral and in ventral view (13, 14); male tergite VIII (8); male sternite VIII (16); female tergite VIII (18); female sternite VIII (19); spermatheca (20). Scale bars: 11, 12, 17, 21: 1.0 mm; 13-16, 18-19: 0.5 mm; 20: 0.2 mm.

Comments: A comparison of the holotype of *P. chinensis* with *P. insignis* from various regions revealed no differences suggesting that it should represent a distinct species. Consequently, *P. chinensis* is here placed in the synonymy of *P. insignis*. For illustrations of the aedeagi of a male from Japan and of the holotype of *P. chinensis*, see ASSING (2001, figs. 6-7) and PACE (1999, figs. 2-3), respectively. The type locality of *P. chinensis* is situated within the known range of *P. insignis*.

The forebody, elytra, ligula, and antenna of this species are illustrated in Figures 1-4 and 11.

Additional material examined:

China: 1♂, Jiangxi prov., Wuyi Shan Nat. Res., Huangganshan, 1800-2050 m, 5.VI.2001, leg. Hlaváč & Cooter (cAss).

Distribution: In China, *Porocallus insignis* was previously known from only two localities, one in Shaanxi (Qin Ling Shan) and one in Sichuan (Qingcheng Shan) (ASSING 2001). It is now known also from two localities in eastern China (Map 1). The specimen from Songshan was collected from moss and litter on the bank of a stream (Guillaume de Rougemont, Londinières, pers. comm. 2003).

3.2. *Porocallus tianmuensis* (Pace, 1999) comb. n.
(Figs. 9-10, 21, Map 1)

Ischyradelia tianmuensis Pace, 1999 (PACE 1999: 108 ff).

Type examined: Holotype ♂: China: Zhejiang Prov., Lin´an County, 1000 m, W. Tianmu Shan N. R. 18.V.1996, J. Cooter / Holotypus Ischyradelia tianmuensis m., det. R. Pace 1996 / Ischyradelia tianmuensis gen. n. sp. n. det. R. Pace 1996 / Porocallus tianmuensis (Pace) det. V. Assing 2003 (MHNG).

Diagnosis: The species is somewhat similar to *P. insignis*, but readily distinguished by the following characters:

Antenna shorter; antennomeres III - X of similar length and approximately as wide as long (Fig. 21). Head, pronotum, and elytra with relatively long, dense, erect pubescence; this pubescence visible especially at lateral margins of pronotum and elytra (Fig. 9). Elytra with very coarse and somewhat granulose puncturation (Fig. 9). Abdomen with very long and dense setae both on dorsal, lateral, and ventral surfaces; tergite VII with relatively coarse puncturation (Fig. 10). Aedeagus with weakly pronounced crista apicalis and with apex of ventral process of characteristic shape especially in lateral view (see PACE 1999, figs. 8-9).

Distribution: *Porocallus tianmuensis* is known only from the type locality in Zhejiang province, eastern China (Map 1).

3.3. *Porocallus hlavaci* sp. n.
(Figs. 5-6, 12-16, Map 1)

Type material: Holotype ♂: China: Fujian prov., Wuyi Shan Nat. Res., Sangan env. (900m), 30.v.-12.vi.2001, Hlaváč & Cooter lgt. / Holotypus ♂ *Porocallus hlavaci* sp. n. det. V. Assing 2003 (cAss).

Description: 5.3 mm. Forebody as in Fig. 5. Head and pronotum blackish; elytra castaneous with the sides weakly infuscated and the scutellum blackish; abdomen blackish brown with the posterior margins of the segments narrowly lighter; legs castaneous; antennae dark brown.

Head about 1.15 times as wide as long (length measured from anterior margin of clypeus); eyes large and prominent; puncturation dense, coarse, and granulose; pubescence short and depressed, barely noticeable (Fig. 5). Antennae relatively short and massive; antennomere II short; IV - VI weakly transverse; X weakly oblong, and XI almost as long as the combined length of IX + X (Fig. 12).

Pronotum 1.22 times as wide as long and 1.25 times as wide as head; puncturation similar to that of head; pubescence depressed and short, but slightly longer than that of head (Fig. 5).

Elytra at suture almost as long as pronotum (Fig. 5); puncturation ill-defined, irregular and confluent everywhere (Fig. 6). Hind wings fully developed. Legs relatively short; metatibia of holotype 0.98 mm; metatarsus very short, only slightly more than half the length of metatibia; metatarsomere I longer than the combined length of II - IV, but shorter than the combined length of II - V.

Abdomen without distinct microsculpture and, especially anteriorly, not very sparse fine puncturation; posterior margin of tergite VII with palisade fringe.

♂: posterior margin of tergite VIII weakly convex (Fig. 15), that of sternite VIII obtusely pointed (Fig. 16); median lobe of aedeagus as in Figs. 13 - 14.

♀: unknown.

Etymology: I dedicate this species to Peter Hlaváč (Košice), who, together with Jon Cooter, discovered it and to whom I am grateful for the generous gift of the holotype.

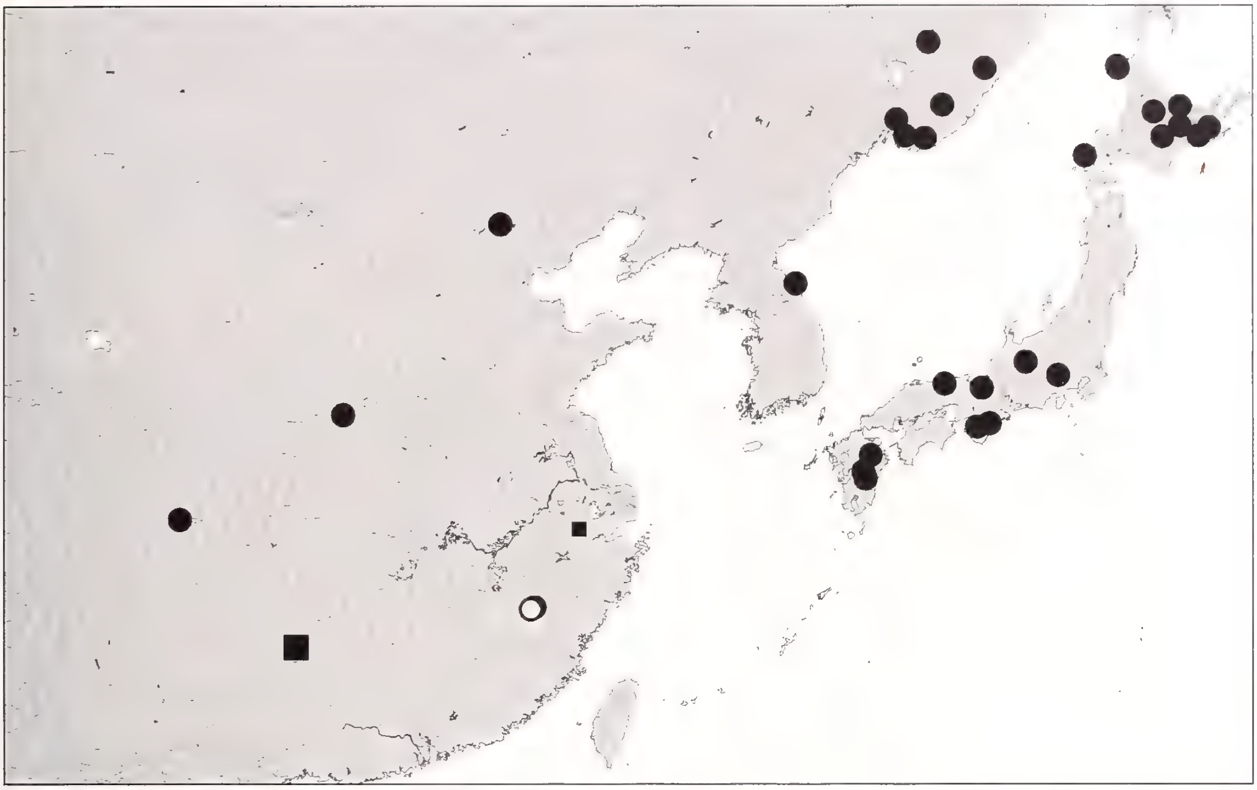
Comparative notes: From *P. insignis*, which, too, was found in the Wuyi Shan Nature Reserve, *P. hlavaci* is readily distinguished especially by the shorter and more massive antenna, the slightly more finely punctate and completely matt appearance of the head and pronotum, the irregular, confluent, and ill-defined puncturation, the matt elytra, the shorter metatibia and metatarsus, the more numerous and longer setae at the sides of the abdomen, and by the morphology of the aedeagus, especially the different shape of the apex of the ventral process in lateral view. From *P. tianmuensis*, it is separated by the much more massive antenna with slightly oblong antennomeres X, the matter appearance of the forebody, the completely different puncturation of the elytra, the shorter metatibia and metatarsus, and by the morphology of the median lobe of the aedeagus. For distinction from the similar *P. ligo* see the following section.

Distribution: The new species is currently known only from one locality in the Wuyi Shan, Fujian Sheng, in southeastern China (Map 1).

3.4. *Porocallus ligo* sp. n. (Figs. 7 - 8, 17 - 20, Map 1)

Type material: Holotype ♀: China: Guizhou, Leishan Co., SE Kaili, NE Leishan, Leigong Shan, E-slope, 26°23.39´N 108°13.33´E / 2.5 km E of pass, 19.6.2001, ca. 1800 m, leg. Schillhammer (14) / Holotypus ♀ *Porocallus ligo* sp. n. det. V. Assing 2003 (NHMW).

Description: 6.6 mm. Facies as in Fig. 7. Coloration as in *P. hlavaci*, but antennae reddish brown.



Map 1. Known distribution of the genus *Porocallus* Sharp: *P. insignis* Sharp (filled circles), *P. hlavaci* sp. n. (open circle), *P. ligo* sp. n. (large square), and *P. tianmuensis* (Pace) (small square).

Head about 1.12 times as wide as long (length measured from anterior margin of clypeus); eyes large and prominent; puncturation dense, coarse, and granulose; pubescence short and depressed, barely noticeable. Antennae relatively long and slender; antennomeres IV-X all clearly oblong; XI shorter than the combined length of IX+X (Fig. 17).

Pronotum about 1.25 times as wide as long and 1.25 times as wide as head (Fig. 7); puncturation similar to that of head; pubescence depressed and short, but longer than that of head.

Elytra at suture almost as long as pronotum; puncturation ill-defined, irregular and confluent everywhere (Fig. 8). Hind wings fully developed. Legs slender; metatibia of holotype 1.18 mm; metatarsus relatively long and slender; metatarsomere I almost as long as the combined length of II - V.

Abdomen shining; posterior margin of tergite VII with palisade fringe.

♂: unknown.

♀: posterior margins of tergite and sternite VIII weakly convex (Figs. 18 - 19); spermatheca with slender capsule (Fig. 20).

Etymology: The name (Lat.) is a noun in apposition and refers to the hoe-like shape of the spermatheca.

Comparative notes: This species is readily distinguished from all its congeners by the slender antennae and by the shape of the spermatheca, from *P. insignis* and *P. tianmuensis* also by the completely matt forebody and by the irregular confluent puncturation of the elytra.

Distribution: *Porocallus ligo* is known from only one locality, the Leigong Shan in Guizhou Sheng, southern China (Map 1), where the holotype was found at an altitude of 1800 m. Its ovaries contained two mature eggs.

4. KEY TO THE SPECIES OF *POROCALLUS*

1. Antenna short and not conspicuously massive, antennomere X about as wide as long (Fig. 21). Elytra with very coarse and dense puncturation (Fig. 9). Forebody with conspicuously dense and (sub-)erect pubescence. Abdominal tergite VII with relatively coarse puncturation (Fig. 10). Aedeagus and spermatheca as figured by PACE (1999: 110). China: Zhejiang (Map 1).................... ***P. tianmuensis*** (Pace)

– Antennae longer and/or conspicuously massive; antennomere X longer than wide. Elytra either with well-defined finer puncturation with shining interstices, or with ill-defined, irregular, confluent puncturation. Forebody with depressed and less dense pubescence. Abdominal tergite VII usually with finer puncturation. Aedeagus of different morphology..... 2

2. Elytra with well-defined puncturation and with shining interstices (Fig. 4); head and pronotum with very weak shine (Fig. 3). Antenna as in Fig. 11. Aedeagus and spermatheca as figured by ASSING (2001, fig. 17). Widespread species known from Japan, the Russian Far East, North Korea, and China (Map 1). .... ***P. insignis*** Sharp

– Elytra with ill-defined confluent puncturation; head and pronotum completely matt. Antenna either distinctly shorter and more massive, or longer and more slender. Species known only from southern China... 3

3. Antennae long and slender, antennomeres IV-X all longer than wide (Fig. 17). Elytra with very subdued shine and with coarser puncturation (Fig. 8). Metatibia and metatarsus long and slender; first metatarsomere almost as long as the combined length of the remaining four tarsomeres. Spermatheca as in Fig. 20. China: Gouizhou (Map 1). ....***P. ligo*** sp. n.

– Antennae short and massive, antennomeres IV-X as wide as long or weakly transverse (Fig. 12). Elytra without shine and with finer puncturation (Fig. 6). Metatarsus short; first metatarsomere distinctly shorter than the combined length of the remaining four tarsomeres. Aedeagus as in Figs. 13-14. China: Fujian (Map 1). ....***P. hlavaci*** sp. n.

Acknowledgements. I am much indebted to Giulio Cuccodoro, Peter Hlaváč, and Harald Schillhammer for the loan and gift, respectively, of the material which this study is based on.

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Received: 22.09.2003
Accepted: 10.12.2004
Corresponding editor: M. Schmitt

Bonner zoologische Beiträge | Band 54 (2005) | Heft 3 | Seiten 103–172 | Bonn, August 2006

Atlas of the Microscopic Hair Structure of Southern African Shrews, Hedgehogs, Golden Moles and Elephant-shrews (Mammalia)

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Abstract. A hair atlas of 41 southern African Macroscelididae, Soricidae, Erinaceidae and Chrysochloridae species is presented and a simple key to identifying those species on the basis of hair characteristics is compiled. Light and electron microscopic hair analyses revealed diagnostic species characteristics such as medullary structure, cross sectional shape and cuticular scale patterns. Additional characteristics like hair colouration, diameter and length as well as geographical distribution have been considered. Hairs of all examined species of golden moles and elephant-shrews show sufficient specific characteristics to allow an unequivocal identification of the species. Shrew hairs, however, lack specific features and in most cases only a definite identification to generic level is possible. The diagnostic criteria of similar keys by other authors as well as limitations of the key are discussed.

Key words. hair fine structure, identification key, hair atlas, small mammals

1. INTRODUCTION

Microscopic analyses of mammalian hair find practical applications in law enforcement and forensic sciences (DE BOOM & DREYER 1953), epidemiology (KEOGH 1979), taxonomy (KEOGH 1975; DUCOMMUN et al. 1994), ecological studies (e.g. DAY 1966; BRUNNER & WALLIS 1986), species conservation, fur and textile industry (WILDMAN 1954) and are also relevant for the identification of food contaminations (KEOGH 1979).

The examination of hairs extracted from regurgitated pellets of birds of prey (MÄRZ 1987) and scats provide information on dietary habits of the respective predators and the existence of mammalian prey (e.g. DAY 1966; GILBERT & NANCEKIVELL 1982; BRUNNER & WALLIS 1986). Since hairs suffer lesser degradation from mastication and digestion than skulls and bones, hairs retain valuable characteristics and are often the only usable remains of an ingested prey species for identification (DAY 1966; BRUNNER & COMAN 1974).

Hairs are usually composed of a cuticula with a layer of scales, the cortex containing pigmentary granules and the medulla (BRUNNER & COMAN 1974). The variations in shape, arrangement and type of these structures as well as characteristics such as hair diameter, distal tip tapering, size ratio between medulla and cortex, etc. are specific for certain taxonomic groups and thus allow the identification of the genus or species from a hair sample when compared to a reference system based on microscopic hair structure such as a hair atlas or an identification key (BRUNNER & COMAN 1974). Certain types of body hairs such as overhairs are of particular diagnostic importance because of the presence of such specific characteristics and structures.

Comprehensive photographic reference systems and identification keys were developed for many mammal species, e. g. of Australia (LYNE & MCMAHON 1951; BRUNNER & COMAN 1974), Asia (AMERASINGHE 1986), northern America (MATHIAK 1938; MAYER 1952; ADORJAN & KOLENOSKY 1969) and Europe (DAY 1966; DZIURDZIK 1973, DEBROT et al. 1982; TEERINK 1991). These also exist for most southern African Bovidae (DREYER 1966; KEOGH 1983), Muridae and Cricetidae (KEOGH 1985) and mammals of the Andries Vosloo Kudu Reserve, South Africa (PERRIN & CAMPBELL 1980).

However, photographic reference systems do not exist for small prey species such as shrews and elephant-shrews as well for most rodent families of southern Africa. The objective of the present study is to compile an atlas of the characteristics and structure of hairs of southern African Macroscelididae, Soricidae, Erinaceidae and Chrysochloridae species as well as a key for their identification based on hair characteristics.

2. MATERIALS AND METHODS

2.1. Collection of reference hair specimens for identification

Hairs were taken from dried skins of the Natural History Museum (MNH), Maputo, Mozambique, the collection of Scientific Services (NKW, KNP), Kruger National Park, Skukuza, South Africa and the Transvaal Museum

(TM), Pretoria, South Africa. Origin and specimen numbers are stated in the Hair Atlas. By means of examination of the teeth, only adult individuals with fully developed pelage were chosen for hair sampling. Hair samples were taken from behind the neck on the back, from the flanks and the belly of the animal. In order to obtain entire unfragmented hairs, a tuft of hairs was clasped with forceps at the base and carefully pulled against the direction of the undisturbed hair. Hair samples were transferred on transparent sticky tape to maintain the original hair orientation and removed for examination by applying a drop of 70% ethanol on the hair sample.

Forty-one species of southern African Macroscelididae (7 spp.), Soricidae (20 spp.), Erinaceidae (1 sp.), and Chrysochloridae (13 spp.) were examined. Hair samples of *Chrysochloris visagiei*, *Chryptochloris zyli* (Chrysochloridae) and *Elephantulus fuscus* (Macroscelididae) were not available from the three collections and therefore not examined.

Taxonomic classification and data on distribution are based on HUTTERER (1993), SCHLITTER (1993), BRONNER (1995) and BOITANI et al. (1999).

2.2. Microscopic analysis of hair samples

Length measurement, description of hair profile and colour was made with the help of a stereo microscope (Wild 195040, Germany) and an electronic calliper (Mitutoyo Digimatic CD-6 CS, Japan). Whole mounts, cross sections and scale casts of hairs were prepared as described in great detail e. g. by BRUNNER & COMAN (1974) and KEOGH (1983, 1985) and examined using a microscope (Olympus T 041, Japan) with phase contrast condenser (Olympus ULW CD 0.30) and phase contrast objectives (Olympus S Plan 10x PL, LWD CD Plan 20x PL, LWD CD Plan 40x PL).

Prior to examination, hair samples were cleaned in 70% ethanol and dried between absorbent tissue paper. For the study of medulla types and pigmentation, temporary mounts were made. Sample hairs were mounted in paraffin oil on cover slip (76 mm x 26 mm x 1 mm) and examined in phase contrast.

Cross sections of the hairs were obtained by the plate method using a stainless steel slide (76 mm x 25 mm x 0.5 mm) with holes of 0.8 mm in diameter. A loop of nylon thread was pushed through a hole and several threads of bright cellulose acetate yarn (335 DTEX, Bembergcell S.P.A., Italy) inserted into the loop as packing material. The nylon thread was pulled through the hole until the cellulose acetate yarn formed a funnel-like structure. A hair sample was inserted into the centre of the "funnel" and pulled into the hole. The protruding parts of the hairs and packing material were cut off on both sides of the slide with a razor blade held at an angle of about 35°. Paraffin oil and a cover slip were placed on the side upon which the second cut was made and the obtained cross section was examined in phase contrast in order to study the shape of cross sections and medulla.

Cuticular scale casts were prepared in order to study cuticular scale patterns. Individual hairs were placed on a thin layer of transparent nail polish on a glass slide. After drying, hairs were removed with forceps and the resulting casts examined in bright field.

Cuticular scale patterns were also examined by the use of a scanning electron microscope. Hair samples were mounted on stubs, coated with gold for two minutes using a sputter coater (Edwards S 150, Germany) at 20 mA and 2.0 x 10^{-3} Pa and scanned with an electron microscope (Zeiss DSM 940A, Germany) at 15.0 KV.

2.3. Measurement of hair diameter and angle of distal hair tip

Photographs of the square compartments (1/400 mm^2) of a counting chamber (Neubauer Lumicyte, Germany) were taken to produce 50 µm scales for all magnifications used in microscopic analyses. The respective scales were used to measure the diameters of hairs on photographs.

For the trigonometric determination of the angle of the distal tip of golden mole hairs, a right-angled triangle was drawn from the respective photographs, measuring 200 µm from the tip of the hair (or the extrapolated point of intersection for hairs with blunt tip) to the right angle.

2.4. Documentation of results

The results were documented with an analogous still camera (Olympus OM-2, Japan) attached to the microscope using colour negative film rated at 100 ISO. The aperture was chosen to obtain relatively long exposure times of about 10 seconds. Thus blurring due to vibrations caused by setting off the shutter could be minimized. During the study of whole mounts and cross sections, additional drawings of hair profiles, medulla types and cross sections shapes were made. For the description and classification of hair characteristics, a simplified scheme was used based on WILLIAMS (1938), BRUNNER & COMAN (1974), PERRIN & CAMPBELL (1980) and KEOGH (1985).

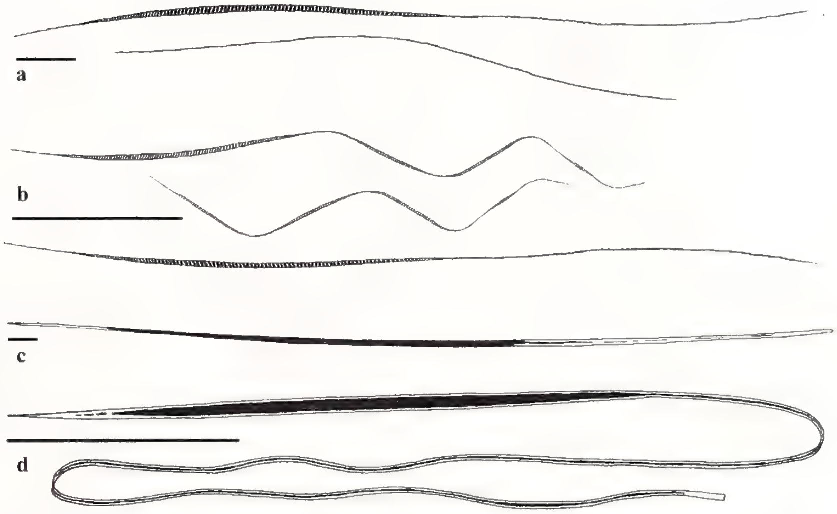

Fig. 1. Basic hair profiles of elephant-shrews (a), shrews (b), hedgehogs (c) and golden moles (d); bars equivalent to 1 mm.

2.5. Hair profiles

Hair profiles were classified according Figure 1 and as suggested i. a. by WILLIAMS (1938) and DREYER (1966). Heavy overhairs are usually long and stiff. Curly overhairs also referred to as shield hairs (BRUNNER & COMAN 1974) or intermediate hairs (PERRIN & CAMPBELL 1980), possess a distally enlarged "shield" region, which is grooved in the case of shrews, golden moles and many Rodent species. The "shield" region often bears specific characteristics and is therefore of diagnostic importance. Furhairs, also referred to as underhairs (BRUNNER & COMAN 1974; PERRIN & CAMPBELL 1980), are shorter, softer and more abundant than overhairs and lack specific features. Other hair types like whiskers were not considered. Unless otherwise stated, the results refer to overhairs having a "shield" region.

2.6. Medulla types

The medulla is the central part of a hair and is embedded in the cortex. The cortical cells, visible only with an electron microscope, grow faster than medullar cells, resulting in medullar air spaces (KEOGH 1983). These air spaces are intransparent for transmission light and thus appear dark, unless "infiltrated", i. e. the contained gas or air is substituted with a suitable medium. Medulla types were studied from whole mounts of hair and classified according to BRUNNER & COMAN (1974), shown in Figure 2. The following medulla types characterize the species examined in the present study:

Wide medulla lattice: This type is the common medulla type of the wider, distal part of golden mole hairs and of some elephant-shrews. The network or lattice is composed of shrunken medulla cells and mostly small, but in the case of a few golden mole species, larger enclosed air spaces. The lattice stretches across the entire diameter of the hair.

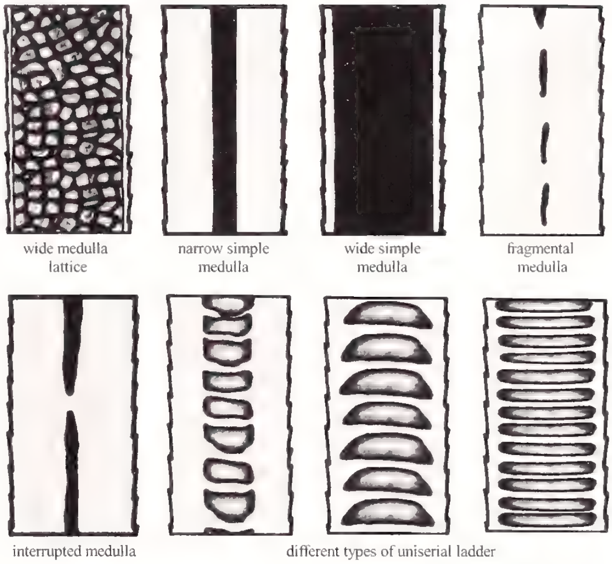

Fig. 2. Medulla types in longitudinal view.

Simple medulla: The medulla lacks an obvious structure and can be narrow or wide. This type is common in hairs of hedgehogs and might be found at the base and tip of shrew hairs.

Fragmental: In this type, the usually simple medulla is repeatedly interrupted by longer sections of cortical material. A fragmental medullary column can be often found at the base of hairs.

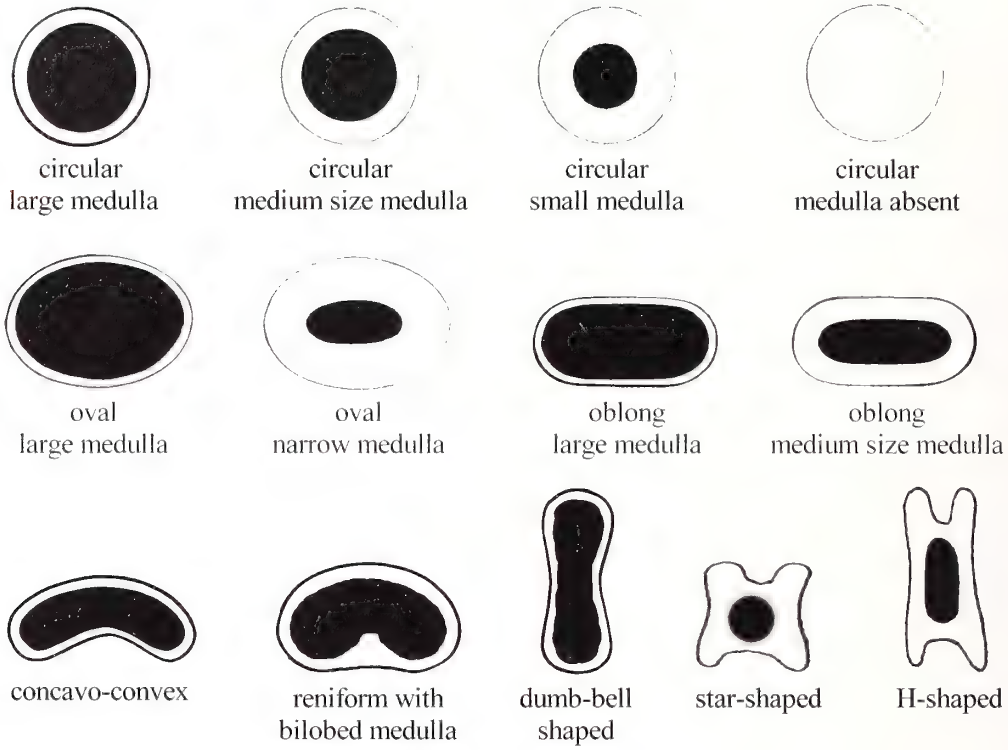
circular
large medulla
circular
medium size medulla
circular
small medulla
circular
medulla absent
oval
large medulla
oval
narrow medulla
oblong
large medulla
oblong
medium size medulla
concavo-convex
reniform with
bilobed medulla
dumb-bell
shaped
star-shaped
H-shaped

Fig. 3. Shapes cross sections of widest part of shield hairs.

Interrupted: The usually simple medulla is interrupted by one or several short sections of cortex material and appears more continuous than the fragmental medulla.

Uniserial ladder: A uniserial ladder medulla is composed of one column of alternating rows of medullar material and air spaces. The "rungs" of the ladder are either regular with parallel elongate, spiral-like, "L" or crescent shaped rungs or irregular with rungs forming letters like "N", "V" or "M". Uniserial ladders are common in underhairs, along the entire overhairs of many small mammals like of shrews and most elephant-shrews and the basal part of golden mole overhairs (DAY 1966).

2.7. Cross sectional shape at widest part of hair

The outer cortex and the central medulla characterize the internal structure of a hair, studied best on cross sections. Unless containing pigment granules, the cortex is of little diagnostic value due to the invisibility of the cortical cells under the light microscope (BRUNNER & COMAN 1974). The cross sectional and medullar shapes, however, are important hair characteristics and were categorized as shown in Figure 3, following WILLIAMS (1938) and BRUNNER & COMAN (1974). According to the medulla width, the shapes can be further divided into large, medium size or small medulla or the medulla can be absent.

Circular shapes are characteristic for cross sections of underhairs, thin basal sections of overhairs and the entire overhair of elephant-shrew hairs and hedgehogs.

Oval and **oblong** shapes characterize cross sections of hairs of hedgehogs, some elephant-shrews and the beginning of the shield region (before the groove) of hairs of some golden moles.

Concavo-convex shapes are typical for cross sections of the shield region of golden mole hairs.

Reniform with bilobed medulla is the shape of cross section found in the wider distal part of overhairs of some elephant-shrews. The concave side is the grooved side.

Dumb-bell shaped cross sections occur in the shield region of shield hairs of shrews and golden moles. The emarginations are the result of shallow longitudinal grooves on both sides of the hair.

Star- and **'H'-shaped** cross sections are typical for the shield region of shrew hairs and may have deep emarginations and prominent extensions of the apices of one or both grooved sides.

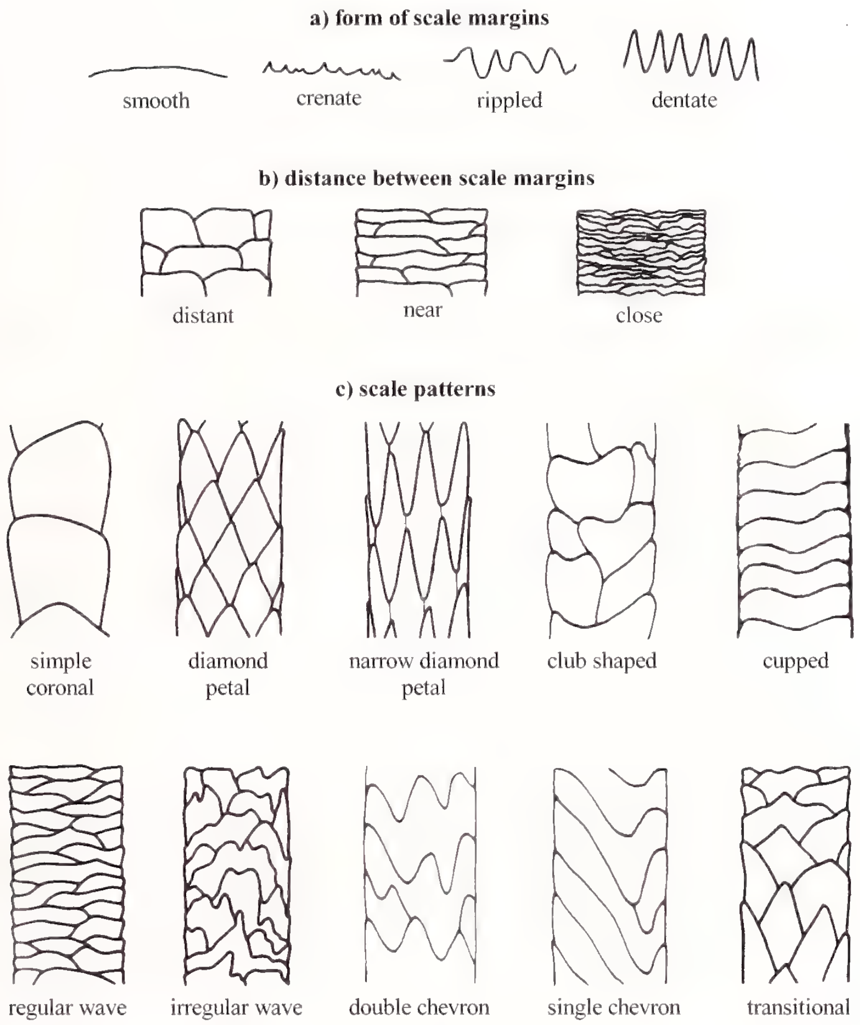
a) form of scale margins
smooth
crenate
rippled
dentate
b) distance between scale margins
distant
near
close
c) scale patterns
simple coronal
diamond petal
narrow diamond petal
club shaped
cupped
regular wave
irregular wave
double chevron
single chevron
transitional

Fig. 4. Cuticular scale patterns.

2.8. Shapes and arrangement of cuticular scales

The cuticle is composed of keratinised overlapping scales, whose patterns, shape, size and types of margins are of diagnostic importance. The classification of scale margins according to Brunner & Coman (1974) refers to the free distal margin of an individual scale according to Figures 4a, b.

Smooth margins form a straight line without indentations.

Crenate margins have shallow but pointed indentations.

Rippled margins are characterized by deeper but rounded indentations.

Dentate margins have tooth-like projections and are typical for petal scales.

The distance between scale margins is characterized by the ratio between width and length of a scale:

Distant scale margins are those with a width of no more than three times of the length.

Near scale margins have a ratio between three and eight.

Close scale margins have a width of more than eight times of the length.

2.9. Cuticular scale patterns

Scale patterns were classified according to Figure 4c following Williams (1938), Brunner & Coman (1974), Perrin & Campbell (1980) and Keogh (1985). The patterns of Lipotyphla, Chrysochloridea and Macroscelidea can be divided into:

Petal scale patterns are formed by a series of overlapping scales with the free distal scale margin slightly raised above the following scale. **Coronal** scale patterns are the common type of the slender base of hairs. They are made of a single or two scales that completely encircle the entire shaft of a hair. The scale margins are smooth and distant. **Diamond petals** are the common scale patterns of the basal part of shrew and elephant-shrew and golden mole hairs, following the coronal hair base. The scale margins are dentate and distant. **Club-shaped** scales are made of a single or two scales reaching across the entire width of a hair and commonly found at the basal part of golden mole hairs. The scale margins are smooth and distant. **Cupped** scale patterns characterize the grooved wider part of overhairs of shrews. This type is made of single scales reaching across the entire diameter. The scale margins are smooth and usually near.

Transitional scale patterns occur at the transition zone between the thinner basal (often diamond petal) and the wider distal part of hairs.

Waved scale patterns commonly occur along the distal wider part of hairs. **Regular waves** usually have smooth and near scale margins. **Irregular waves** have rippled or crenate margins with deeper emarginations, the distance between the scale margins can be near or close. **Chevron** scale patterns have more or less regular, parallel scale margins with one (single) or two (double) 'V'-like crests and are composed of two or more scales. This type can be found in the thinner basal part of some elephant-shrew and golden mole hairs.

3. RESULTS AND DISCUSSION

This Hair Atlas provides a key for the identification of 41 species of southern African Lipotyphla, Chrysochloridea and Macroscelidea based on their hair characteristics. Hair characteristics allowing definite species-level identification was found for the hedgehog *Atelerix frontalis*, some Macroscelid species (*Petrodromus tetradactylus*, *Macroscelides proboscideus*, *Elephantulus brachyrhynchus*) and some golden moles species (*Chrysopalax* spp., *Amblysomus* spp., *Chrysochloris asiatica*, *Calcochloris obtusirostris*, *Cryptochloris wintoni*). The unmistakable identification of all Macroscelidea and all golden moles was possible, when geographic distribution data were used in addition to hair characteristics. However, some shrew species were not identified unequivocally, even when combining hair characteristics with geographic distribution.

Other authors also reported of the unavailability of specific hair characteristics for some species (PERRIN & CAMPBELL 1980; KEOGH 1985). Therefore, it has been suggested that a more reliable identification can be obtained by combining geographic distribution of a species with hair characteristics (BRUNNER & COMAN 1974; PERRIN & CAMPBELL 1980).

Most species examined in the present study showed common generic characteristics, e. g. the hair length of the shrew genera *Myosorex* (7 mm to 9 mm), of *Suncus* (3 mm to 6 mm) and of *Sylvisorex* (about 7 mm). Almost all species of *Crocidura* have hairs with coronal scale patterns at their distal tip whereas this characteristic is less consistent in the other examined shrew genera. Additionally, shield hairs of the genus *Myosorex* usually have five constrictions and the hair length was more homogenous than in other shrew genera. Some genera of golden moles also showed distinct genus specific features, e.g., much longer hairs in the case of *Chrysopalax*. Within the elephant-shrews, the medulla type was not specific for the genus *Elephantulus*. Whole mounts of overhairs of *E. myurus* and *E. brachyrhynchus* revealed medulla lattice, whereas all other species of this genus had a medulla with uniserial ladder.

Hair characteristics of the four studied families are always very typical and allow a definite identification of the family. Such family specific characteristics for instance were the hair profile and the shape of hair cross sections for golden moles and shrews as well as the cupped cuticular scale patterns of the distal part of overhairs of all shrew species. This is in accordance with specific features of moles and shrews found by WILLIAMS (1938) and shrews described by DANNELID (1986). The results of the present study are also in conformity with the study of the hair morphology of the shield region of curly overhairs of various shrew genera (DUCOMMUN et al. 1994). Shallow V- or U-shaped notches were also found along the shield region of *Crocidura* and *Suncus* in the present study (e.g., Pl. 8N, 9N, 10K, 11N, 12N and Pl. 25N & O, 26L), whereas the *Myosorex* shield is deeply grooved (Pl. 20F, 21G, 22N). Additionally, both studies show similar scale patterns on the shield region of *C. luna* and *Sylvisorex megalura*.

Hair characteristics of some of the species included in the present study have already been described by PERRIN & CAMPBELL (1980). Apart from using different terms to classify hair profiles and scale patterns, the study of these authors was mainly based on cuticular scale patterns. Despite the differences in methodology, both studies show similar results; e.g., for *Atelerix frontalis*, *Crocidura cyanea* and *C. flavescens*. Regarding the study of PERRIN & CAMPBELL (1980), the petal scale pattern in the fine region and the flattened mosaic at the midpoint of the shield region of *Macroscelides proboscideus* hair correspond with the transitional scale pattern between the narrow diamond petal and regular wave patterns (distal part of Pl. 6 M) and the regular scale pattern (Pl. 6 N) of the present study. PERRIN & CAMPBELL (1980) solely used cuticular scale patterns of the shield region to differentiate between golden moles. However, in the present study additional characteristics like cross sections and geographical distribution were used to discriminate more reliably between these species.

The hair characteristics used in the present study are based on the longitudinal view of the medulla, cross sectional shape of hair and medulla, medulla and cortex pigmentation, cuticular scale pattern, angle of distal hair tip, constrictions of hairs as well as hair profiles, colouration, length, minimum and maximum diameter. The consideration and use of certain hair characteristics is controversial and largely depends on the author. In the present study a combination of various hair characteristics along the entire hair was studied in order to overcome the shortcomings of the one or the other feature.

Regarding characteristics related to the medulla structure, KEOGH (1983) argues that the medulla varies considerably along the length of the hair and between individuals of the same species, and therefore this feature was not included in her study. On the other hand, WILLIAMS (1938), DAY (1966) and BRUNNER & COMAN (1974) stress the importance of a number of medulla characteristics. Some authors (BRUNNER & COMAN 1974; KEOGH 1983) even include the “infiltrated” medulla in which the air or gas of the air spaces has been substituted with mounting medium. In the present study, a simplified classification system of the longitudinal view of the medulla according to BRUNNER & COMAN (1974) has proven to be of diagnostic value, particularly in combination with other hair characteristics.

The cross sectional shape of a hair and the medulla are widely used in hair analyses (WILLIAMS, 1938; DREYER 1966; BRUNNER & COMAN 1974; KEOGH 1983). As described by BRUNNER & COMAN (1974) and found in the present study, cross sectional shapes in particular are prominent features characterizing hair of shrews and golden moles. Furthermore, with the help of cross sections the longitudinal grooves along the shield region of shield hairs of shrews and golden moles can be easily studied. Grooves were also considered of diagnostic importance for the identification of Cricetidae and Muridae by PERRIN & CAMPBELL (1980) and KEOGH (1985). However, the preparation of cross sections is delicate and requires a skilled operator (BRUNNER & COMAN 1974), particularly when dealing with short hairs as those of shrews.

Cuticular scale patterns are another diagnostic feature used in the present and many other studies (e.g., DREYER 1966; BRUNNER & COMAN 1974; PERRIN & CAMPBELL 1980; KEOGH 1983; KEOGH 1985). According to DAY (1966), cuticular scale patterns of the basal region of hairs are characteristic and thus useful for hair identification. In the present study, however, scale patterns were rarely found to be species-specific but were in most cases characteristic for genera or the entire family. Even electron microscopic scans did not reveal more detail of the cuticular scales than did light microscopy, as the comparison shows (Pl. 42). Therefore, the much faster, cheaper and simpler light microscopy was used for the examination of scale patterns.

Even though the use of hair length is a controversial characteristic, length together with minimum and maximum hair diameter were used in the present study and specifically for some of the golden mole species and shrew genera. Hair length was also used by MATHIAK (1938), MAYER (1952) and KEOGH (1983 & 1985), but since this feature might be subject to large individual variations, DREYER (1966) and other authors only considered the minimum and maximum hair diameter.

For similar reasons, pigmentation of hairs has not been used widely as a characteristic; however, there are a number of authors employing this feature (e.g., DREYER 1966; KEOGH 1983). According to BRUNNER & COMAN (1974), hair pigmentation is not of primary diagnostic importance, but can be used to confirm an identification made on the basis of other features. In the present study, colouration of entire hairs as well as of the cortex and medulla in cross sections were considered, despite the fact that colour might vary according to the age of the animal and the season of the year (PERRIN & CAMPBELL 1980). In order to minimize colour variations of different body parts, hairs from the back, flanks and belly of the animal were described. Additionally, colour charts can be used to minimize subjective interpretation of the hair colour (MAYER 1952).

Identification keys based on hair characteristics have a number of limitations (e.g., DAY 1966; BRUNNER & COMAN 1974; PERRIN & CAMPBELL 1980). The most criticised shortfalls are the variations of hair characteristics with age, sex, diet, body part, geographic origin, season of the year, etc.

BRUNNER & COMAN (1974) studied the different stages of hair development and showed that the hair, once protruded above the skin, is fully differentiated and no longer subject to further morphological changes. KEOGH (1975) found that season, sex and diet had no effect on cuticular scale patterns of rodents. According to the same author, variations of scale patterns solely depended on the age of an individual and after six months of age, the scale pattern remained constant. According to BRUNNER & COMAN (1974), the development of the pelage of *Rattus norvegicus* is completed after three months of age. A comprehensive study of the Bovidae *Tragelaphus strepsiceros*, *Aepyceros melampus*, *Sylvicapra grimmia* and *Gorgon taurinus* did not reveal any differences in cuticular scale patterns, pigmentation and hair profiles between adult males and females (DREYER 1966). However, this author found higher variations of the cuticular scale patterns in subadult Kudus. Different to this, DAY (1966) noticed that subadults of small mammals showed similar cuticular scale patterns to adult animals, but these patterns were expressed in a simplified form. In order to minimize the influence of age on certain hair characteristics, only adult animals were used in the present study for hair sampling and the subsequent hair analyses.

Morphological differences between hair types and samples taken from different body parts can be considerable and are particularly pronounced in whiskers, ornamental hairs, hairs of legs, tail, etc. (DE BOOM & DRYER 1953; DAY 1966; BRUNNER & COMAN 1974). Hairs of the body trunk, however, show more uniform characteristics and therefore are more suitable for hair studies. As done in the present study, the difficulty arising from variations in hairs of different body parts can be overcome by including hairs of several parts of the trunk. In the present study hair samples of different body parts commonly vary in colour. A hair characteristic typical for hair of a certain part of the trunk could be found only in a single instance, the concavo-convex cross sections of ventral hairs of *Chrysochloris asiatica* (Pl. 35 D).

Individual morphological variations of hair structure render an unequivocal identification of a certain species more difficult (BRUNNER & COMAN 1974). Therefore, PERRIN & CAMPBELL (1980) suggest the sampling of hairs derived from different individuals of the same species. Additionally, hair development and the resulting hair characteristics can vary with the geographic origin of a hair sample, particularly with the prevailing climate and habitat (e.g., DREYER 1966; PERRIN & CAMPBELL 1980) so that samples of various origins are recommended (PERRIN & CAMPBELL 1980).

The process of digestion usually causes little alteration of the hair structure of a consumed mammal (BRUNNER & WALLIS 1986) and thus, photographic reference systems and identification keys can be based on hair samples; e. g., taken from museum skins (BRUNNER & COMAN 1974). DAY (1966) suggests the additional analysis of teeth and skeletal remains contained in predator scats would confirm the identification of the prey species based on hair examinations.

Finally, the revision of the genus *Amblysomus* (BRONNER 1995) is supported by the findings of the present study: *A. hottentotus* and *A. iris* differ from *Neamblysomus gunningi* and *N. julianae* in terms of hair diameter and shape of cross section. The same author also separated *Carpitalpa arendsi* from the genus *Chlorotalpa*. Even though having some similar hair characteristics such as maximum diameter and shape of cross section, *C. arendsi* has double chevron scale patterns and thus differs from *Chlorotalpa duthieae* and *C. sclateri*, as shown by the present study. The comparison of hair samples of *Crocidura bicolor* with *C. fuscomurina* showed identical hair characteristics and therefore supports the assemblage of the two species as *C. fuscomurina* (HUTTERER 1993). The revision of the formerly separated species *Crocidura olivieri occidentalis* and *C. olivieri martiensseni* (HUTTERER 1993), is not supported by the findings of the present studies, since the examined hairs differ quite considerably in hair length, diameter and scale patterns.

4. HAIR ATLAS OF SOUTHERN AFRICAN ELEPHANT-SHREWS, SHREWS, HEDGEHOGS AND GOLDEN MOLES

4.1. Order Macroscelidea

Family Macroscelididae (elephant-shrews, sengis)

Elephant-shrews have long overhairs that are wider at their distal part (Fig. 1a). Underhairs are long, soft, sometimes constricted and more abundant than overhairs. Hairs occasionally have an intumescence at the distal part. Cross sections of hairs are almost always circular, the medulla has a uniserial ladder and some species have wide lattice at the distal part of hair. Scale patterns of distal hair part are regular or irregular waves, the distal tip often is of coronal type. Unless indicated, the described hair characteristics refer to both types of hairs.

Elephantulus brachyrhynchus (A. Smith, 1836) Short-snouted elephant-shrew (Pl. 1)

Origin of hair sample: MHN: junction Sabi-Lundi south bank, Mozambique (*Nasilio brachyrhynchus*); NKW 4: Mwambia Pan, KNP, South Africa.

Hair colour: Dorsal hairs dark red at base and dark brown at the distal part; hairs of the flanks dark at base and dark red at the distal end; ventral hairs dark grey basally and brownish-yellow at distal part.

Hair types, shape and length: Overhairs long and thick, underhairs relatively thin and constricted. Hairs sometimes with intumescences (F, G) at distal part. Length of overhairs about 15.5 ± 1.1 mm (n = 9); maximum hair diameter 58 µm, minimum diameter about 19 µm.

Description of whole mounts: Overhairs basally with uniserial ladder (B, C), wide medulla lattice at distal part (D-F) and distally ending with simple medulla (H). Generally, the distal parts have transparent and slightly thickened areas (D, F). Underhairs with uniserial ladder with crescent-shaped rungs distally (A).

Form of scale margins: Basally smooth (J, K), dentate (L-N), smooth (O), crenate (P) and smooth (Q-S) at distal hair tip.

Distance between scale margins: Scale margins near at base (basal part of J), distant (distal part of J-N), near (O) and close (P-S) at distal hair tip.

Cuticular scale patterns: Basally simple coronal scale patterns (J, K), narrow diamond petal (L, M), diamond petal/transitional (N), regular waves (O), irregular waves (P) and regular waves (Q-S) at distal hair tip.

Description of cross sections: Circular cross sections with large medulla (Ia) or medium size medulla (Ib); medulla always dark; cortex of some cross sections orange or gold, resulting in an intense brilliant sheen of the cortex in transmitted light of microscope (Ib); cortex and medulla of other cross sections dark (Ic).

Elephantulus edwardi (A. Smith, 1839) Cape rock elephant-shrew (Pl. 2)

Origin of hair sample: TM 687: Hannover, Central Prov., South Africa.

Hair colour: Dorsal hairs dark grey basally and light brown at distal part; hairs of flanks and belly basally grey and light brown at distal part.

Hair types, shape and length: Overhairs relatively long and thick and less abundant than underhairs; underhairs thin and sometimes constricted. Length of overhairs about 14.3 ± 0.8 mm (n = 4); maximum hair diameter 30 µm, minimum diameter about 15 µm.

Description of whole mounts: Medulla with uniserial ladder (A-E) along entire hair, distally rungs crescent-like (C) and L-shaped (D).

Form of scale margins: Smooth at base (G, H), dentate (I, basal part of J) and smooth (distal part of J-N) at distal hair tip.

Distance between scale margins: At base near (basal part of G), distant scale margins (distal part of G, H-J) and near (K-N) at distal hair tip.

Cuticular scale patterns: Basally simple coronal scale patterns (G, H), narrow diamond petal (I, J), transitional (distal part of J), regular waves (K-M) and coronal (N) at distal hair tip.

Description of cross sections: Circular shapes of cross sections with medium size to large medulla (Fa); medulla and cortex of some cross sections light brown, some cross sections with lighter medulla and darker cortex (Fa) or vice versa, or medulla and cortex of other cross sections black (Fb).

Elephantulus intufi (A. Smith, 1836) Bushveld elephant-shrew (Pl. 3)

Origin of hair sample: TM 15239: Nguia, Botswana Reserve, Botswana.

Hair colour: Dorsal hairs dark grey at basal part and dark red distally; hairs of flanks and belly dark grey at basal part and light red distally.

Hair types, shape and length: Overhairs relatively long and wider along distal part; underhairs thinner and sometimes constricted. Hairs sometimes with intumescence (D) at distal part. Length of overhairs about 14.7 ± 0.5 mm (n = 6); maximum hair diameter 53 µm, minimum diameter about 21 µm.

Description of whole mounts: Overhairs basally with uniserial ladder /simple medulla (B, C) and simple at distal part (D-F). Medulla of underhairs with uniserial ladder with spiral-like rungs (A).

Form of scale margins: Smooth at base (H, I) dentate (J, basal part of K) smooth/crenate (distal part of K, L, M) and smooth (N, O) at distal hair tip.

Distance between scale margins: Scale margins near at base (H), distant (distal part of H, I-K) and near (L-O) at distal hair tip.

Cuticular scale patterns: Basally simple coronal scale patterns (H and I), narrow diamond petal (J), diamond petal/transitional (K), regular waves (L, M) and coronal (N, O) at distal hair tip.

Description of cross sections: Circular shapes of cross sections with medium size medulla or large medulla (Gc); medulla and cortex of some cross sections light brownish-grey (Gb, c), medulla and cortex of other cross sections dark (Ga).

Elephantulus myurus Thomas & Schwann, 1906 Rock elephant-shrew (Pl. 4)

Origin of hair sample: NKW 18: Pafuri, KNP, South Africa; NHM: junction Sabi-Lundi, south bank, Mozambique; TM 39049: Moshanens, Botswana.

Hair colour: Dorsal hairs grey at basal part and dark red distally; hairs of flanks grey at basal part and distally dark red with a brown hue; ventral hairs grey at basal part and light yellow distally.

Hair types, shape and length: Overhairs relatively long, underhairs thinner and constricted. Hairs sometimes with intumescences along distal part (F). Length of overhairs about 12.0 mm ± 0.8 (n = 9); maximum hair diameter 46 µm, minimum diameter about 15 µm.

Description of whole mounts: Overhairs basally with uniserial ladder (C, D), wide medulla lattice (E) and simple medulla (F, G) at distal part and occasionally with protuberances at distal part (F). Underhairs of uniserial ladder along the entire hair (A, B), sometimes constricted (A).

Form of scale margins: Smooth (H, I) at base, dentate (J) and smooth (K-N) at distal hair tip.

Distance between scale margins: Scale margins near at base (H), distant (distal part of H, I, J), near (K) and close (L-N) at distal part of hairs.

Cuticular scale patterns: Basally simple coronal scale patterns (H, I), narrow diamond petal (J), regular waves (K-M) and coronal (N) at distal hair tip.

Description of cross sections: Circular shapes of cross sections with large medulla (Oa); medulla and cortex of some cross sections light brown (Oa), medulla and cortex of other cross sections dark (Ob).

Elephantulus rupestris (A. Smith, 1830) Smith's or Western rock elephant-shrew (Pl. 5)

Origin of hair sample: TM 10218: Tsabis, West of Rochboth, Botswana.

Hair colour: Dorsal hairs grey at basal part and dark red distally; hairs of flanks grey at basal part and light red distally; ventral hairs dark grey at basal part and light yellow distally.

Hair types, shape and length: Overhairs relatively long and distal part wider; underhairs thinner and quite long. Length of overhairs about 18.2 ± 0.8 mm (n = 6); maximum hair diameter 34 µm, minimum diameter about 18 µm.

Description of whole mounts: Medulla of underhairs (A) and overhairs (B-H) with uniserial ladder along the entire hair; rungs distally crescent-shaped (F, G, H) and occasionally with transparent parts (D, F); distal tip without medulla (H).

Form of scale margins: Smooth at base (J-L), dentate (M-O), smooth (P, Q), crenate (R) and smooth (S) at distal hair tip.

Distance between scale margins: Scale margins near (J) at base, distant (K-P) and near (Q-S) at distal hair tip.

Cuticular scale patterns: Basally simple coronal scale patterns (J-L), narrow diamond petal (M-O), transitional (P), regular waves (Q, R) and coronal (S) at distal hair tip.

Description of cross sections: Circular shapes of cross sections with medium size (Ia) to large medulla (Ib); medulla and cortex of some cross sections light brown, resulting in a weak golden sheen of the cortex in transmitted light of microscope (Ib), some cross sections with more or less transparent cortex and dark medulla (Ia) or dark cortex and medulla.

Macroscelides proboscideus (Shaw, 1800) Round-eared or short-eared elephant-shrew (Pl. 6)

Origin of hair sample: TM 28146: Faron Kongras, Springbok Game Reserve, Transvaal, South Africa.

Hair colour: Dorsal and lateral hairs dark grey at basal part and dark red distally; ventral hairs dark grey at basal part and light yellow distally.

Hair types, shape and length: Hairs relatively long and thin, distal part of overhairs wider, underhairs thinner. Hairs sometimes with intumescence (F) at distal part. Length of overhairs about 18.1 ± 0.9 mm (n = 4); maximum hair diameter 26 µm, minimum diameter about 9 µm.

Description of whole mounts: Medulla of all hairs with uniserial ladder (A-F) along the entire hair; distally rungs 'L'-shaped (D, E), occasionally with transparent parts (C), with protuberances (F) and with intransparent distal hair tip (G).

Form of scale margins: Smooth (I, J) at base, dentate (K, L, basal part of M) and smooth (distal part of M-Q) at distal hair tip.

Distance between scale margins: Scale margins near at base (I), distant (distal part of I-M), near (N, O) and close (P, Q) at distal hair tip.

Cuticular scale patterns: Basally simple coronal scale patterns (I, J), narrow diamond petal (K-L), transitional (M), regular waves (N-P) and coronal (Q) at distal hair tip.

Description of cross sections: Circular shapes of cross sections with medium size medulla or large medulla (Ha); medulla and cortex of some cross sections transparent (Hb) or with more or less transparent cortex and dark medulla, resulting in a weak sheen of the cortex in transmitted light of microscope (Ha); some cross sections with dark cortex and medulla.

Petrodromus tetradactylus Peters, 1846 Four-toed elephant-shrew (Pl. 7)

Origin of hair sample: NKW10: Tussen, Magabene, Makembane KNP, South Africa; NHM: north bank Sabi, Mozambique.

Hair colour: Dorsal hairs grey at basal part and dark red distally; hairs of flanks grey at basal part and red with a yellow hue distally; ventral hairs vary from dark to light red.

Hair types, shape and length: Overhairs relatively long and thick, distal part wider; underhairs thinner and occasionally with constrictions. Hairs sometimes with intumescence (B, F) at distal part. Length of overhairs about 17.5 ± 0.5 mm (n = 9); maximum hair diameter 59 µm, minimum diameter about 21 µm.

Description of whole mounts: Medulla at base of overhairs with uniserial ladder with oblique, "V"-shaped rungs (E, G); further distally, rungs resembling "letters" (H) and with simple medulla towards distal hair tip (I, J). Medulla of underhairs with uniserial ladder (A-C), at distal part with crescent-shaped rungs (C).

Form of scale margins: Smooth at base (L), dentate (M-O), smooth/crenate (P), rippled (Q) and smooth (R, S) at distal hair tip.

Distance between scale margins: Scale margins near (L) at base, distant (distal part of L-O) and close (P-S) at distal hair tip.

Cuticular scale patterns: At base simple coronal scale patterns (L), narrow diamond petal (M, N); diamond petal/transitional (O), regular waves (P), irregular waves (Q) and regular waves (R, S) at distal hair tip.

Description of cross sections: Circular shapes of cross sections with large medulla (Ka) or medium size medulla (Kb); medulla and cortex of some cross sections light brown, resulting in an intense brilliant sheen of the cortex in transmitted light of microscope (Ka, b); other cross sections dark medulla and dark cortex (Kc).

4.2. Order Soricomorpha

Family Soricidae (shrews)

The pelage of shrews is soft and plush-like, the hairs (Fig. 1b) are relatively short. Curled overhairs (shield hairs) usually have one or two constrictions and a flattened, expanded distal part of the hair with a pronounced longitudinal groove on one or both surfaces. Heavy overhairs are straight, longer, lack constrictions and are rare in number. Underhairs have a thin distal end and several constrictions, at which the hair changes its direction (Pl. 13 H), resulting in a zigzag-like shape. Cross sections of hairs are typically rectangular or quadrangular with emarginations of several sides resulting in a dumb-bell shaped, "H"-like or star-like outline (Fig. 3); the medulla has uniserial ladder. Scale patterns of grooved part of shield region are always cupped, the hair tip has with coronal or regular waves. Unless indicated, the described hair characteristics refer to overhairs with shield region (shield hair).

Crocidura cyanea (Duvernoy, 1838) Reddish-grey musk shrew (Pl. 8)

Origin of hair sample: NKW 2: Malelane, KNP, South Africa.

Hair colour: Dorsal and lateral hairs light grey at basal part and greyish-brown distally; ventral hairs light grey.

Hair types, shape and length: Heavy overhairs straight and without constrictions; curled overhairs (shield hairs) with thickened and grooved distal part and two constrictions; underhairs thinner and undulating at constrictions. Length of overhairs about 6.2 ± 0.5 mm (n = 7); maximum diameter of shield region 29 µm, minimum diameter about 7 µm.

Description of whole mounts: At base simple medulla (A), further distally uniserial ladder (B-F) with regular and straight rungs (D, E) or less regular, 'mushroom' -shaped rungs (F) ending in a transparent distal hair tip (G).

Form of scale margins: Smooth (I, J) at base, dentate (K, L), smooth (M, N), crenate (O, P) and smooth (Q) at distal hair tip.

Distance between scale margins: Scale margins at base close, further distally distant (I-M), near (N) and close (O-Q) at distal hairs tip.

Cuticular scale patterns: At base simple coronal (I, J), further distally narrow diamond petal (K), diamond petal (L), regular waves (M), cupped (N), irregular waves (O, P) and coronal (Q) at distal hair tip.

Description of cross sections: Rectangular shaped outline of cross section with slightly invaginated sides (Ha), "H"-shaped outline with more or less pronounced extensions (Hb), both with large medulla, other outlines of cross sections circular with medium size medulla (Hc); medulla black or grey, cortex brown, light or dark grey.

Crocidura flavescens (Geoffroy, 1827) Greater red musk shrew (Pl. 9)

Origin of hair sample: TM 9000: Krysna Distr. Deepwalls, Cape Province, South Africa.

Hair colour: Hairs light grey at basal part and dark brown to greyish-brown distally.

Hair types, shape and length: Heavy overhairs straight and without constrictions; curled overhairs (shield hairs) with thickened and grooved distal part and two or three constrictions; underhairs thinner and undulating at constrictions. Length of overhairs about 5.5 ± 0.2 mm (n = 5); maximum diameter of shield region 35 µm, minimum diameter about 6 µm.

Description of whole mounts: At base simple medulla (A, B); further distally uniserial ladder (C-E), sometimes irregular forming 'letters' (D, E) and ending in a thin transparent distal tip (F).

Form of scale margins: At base smooth (H, I), dentate (J-L), smooth (M, N) and rippled (O, P) at distal hair tip.

Distance between scale margins: Scale margins near (H) at base, distant (I-L), near (M, N) and close (O, P) at distal hair tip.

Cuticular scale patterns: At base simple coronal (H, I), further distally narrow diamond petal (J, K), diamond petal (L), transitional (M), cupped (N) and irregular waves (O, P) at distal hair tip.

Description of cross sections: Cross sections predominantly rectangular shaped with slight emarginations of all sides resulting in short extensions of one or both short sides (Ga), dumb-bell shaped (Gb), trapezoidal (Gc, d) or circular outlines (Ge, Qa); all cross sections with medium size to large medulla; medulla black or grey, cortex brown, light or dark grey, sometimes with a brilliant sheen in transmitted light of microscope (G).

Crocidura fuscomurina (Heuglin, 1865) Tiny musk shrew (Pl. 10)

Origin of hair sample: NKW 1: Skukuza, KNP, South Africa; TM 45738: Vryburg Distr., Mopolo Nat. Res., North West Province, South Africa; TM 37158 (*C. bicolor*): Pietermaritzburg Distr., Natal, South Africa.

Hair colour: Hairs dark grey at basal part and light brown to dark brown distally.

Hair types, shape and length: Heavy overhairs straight and without constrictions; curled overhairs (shield hairs) with thickened and grooved distal part and one or two constrictions; underhairs thinner and undulating at constrictions. Length of overhairs about 2.7 ± 0.1 mm (n = 5); maximum diameter of shield region 26 µm, minimum diameter about 6 µm.

Description of whole mounts: At base simple medulla (A); further distally uniserial ladder (B-D), at distal part with slightly oblique rungs (C, D), ending in a thin transparent distal hair tip (E).

Form of scale margins: Smooth at base (G, H), further distally smooth/crenate (I-K), rippled (L) and smooth (M) at distal hair tip.

Distance between scale margins: Scale margins near (basal part of G), distant (distal part of G, H) at base, near (I, J) and close (K-M) at distal hair tip.

Cuticular scale patterns: At base simple coronal (G, H), at distal part regular waves (I, J), cupped (K), irregular waves (L) and coronal (M) at distal hair tip.

Description of cross sections: Cross sections predominantly quadrangular or rectangular shaped with slight emarginations of the short sides resulting in prominent extensions of these sides (Fa) or circular (Fb) shapes in outline; all cross sections with small or medium size medulla; medulla black or grey, cortex brown, light or dark grey.

Crocidura hirta Peters, 1852 Lesser red musk shrew (Pl. 11)

Origin of hair sample: NKW 13: Pafuri, KNP, South Africa; MHN: Maringa, Sabi north bank, Mozambique.

Hair colour: Hairs dark grey at basal part and light brown to brownish-grey distally.

Hair types, shape and length: Heavy overhairs straight and without constrictions; curled overhairs (shield hairs) with thickened and grooved distal part and three constrictions; underhairs thinner and undulating at constrictions. Length of overhairs about 5.5 ± 0.2 mm (n = 7); maximum diameter of shield region 33 µm, minimum diameter about 6 µm.

Description of whole mounts: At base simple medulla (A), further distally uniserial ladder (B-G), rungs sometimes irregular and "V"-shaped (E) or "mushroom"-like (D, F), ending in a thin transparent distal hair tip (G).

Form of scale margins: Smooth at base (I), further distally dentate (J, K), smooth (L), rippled (M, N), crenate (O) and smooth (P) at distal hair tip.

Distance between scale margins: Scale margins at base close; distant (I-L), near (M, N) and close (O, P) at distal hair tip.

Cuticular scale patterns: At base simple coronal (I), further distally narrow diamond petal (J, K); transitional (L), cupped (M), irregular waves (N, O) and coronal (P) at distal hair tip.

Description of cross sections: Cross sections dumb-bell shaped in outline with emarginations of the long sides with prominent extensions (Ha) or round short sides (Hb) and circular in outline (Hc); cross sections with medium size to large medulla, sometimes emarginated, reflecting the shape of the cross section; medulla black or grey, cortex brown, light or dark grey, sometimes with a brilliant sheen in transmitted light of microscope (Ha).

Crocidura luna Dollman, 1910 Greater grey-brown musk shrew (Pl. 12)

Origin of hair sample: TM 7728: Mt. Selinda, Melsetter Distr., Zimbabwe.

Hair colour: Dorsal and ventral hairs dark grey at basal part and light brown distally, lateral hairs dark grey at basal part and dark brown distally.

Hair types, shape and length: Heavy overhairs straight and without constrictions; curled overhairs (shield hairs) with thickened and grooved distal part and three constrictions; underhairs thinner and undulating at constrictions. Length of overhairs about 6.7 ± 0.5 mm (n = 5); maximum diameter of shield region 31 µm, minimum diameter about 11 µm.

Description of whole mounts: Hairs lack medulla at base (A), further distally fragmental simple medulla (B) and uniserial ladder (C-F), sometimes with irregular and "N" or "V"-shaped rungs (E), ending in a thin transparent distal hair tip (G).

Form of scale margins: Smooth at base (I, J), dentate (K-M), smooth (N), rippled (O) and smooth (P) at distal hair tip.

Distance between scale margins: Scale margins near (I) at base, distant (J-M), near (N) and close (O, P) at distal hair tip.

Cuticular scale patterns: At base simple coronal (I-K), further distally narrow diamond petal (L), diamond petal/transitional (M), cupped (N), regular waves (O) and coronal (P) at distal hair tip.

Description of cross sections: Cross sections predominantly rectangular shaped in outline with emarginations of all sides with prominent extensions (Ha, Hb, Qa), dumb-bell shaped (Qb), quadrangular shaped with concave sides resulting in a star-like shape (Hc) or trapezoidal (Qc), others circular in outline (Hd); cortex and medulla clearly separated; all cross sections with medium size or large medulla, sometimes emarginated (Hb), reflecting the shape of the cross section; medulla black or grey, cortex brown, light or dark grey, sometimes with a brilliant sheen in transmitted light of microscope (Ha, b, Qa-c).

Crocidura maquassiensis Roberts, 1946 Maquassie musk shrew (Pl. 13)

Origin of hair sample: TM 40460: Kosi Lake, Dept. of Health Camp, Natal, South Africa.

Hair colour: Hairs dark grey at basal part and light brown distally.

Hair types, shape and length: Heavy overhairs straight and without constrictions; curled overhairs (shield hairs) with thickened and grooved distal part and two constrictions; underhairs thinner and undulating at constrictions (H). Length of overhairs about 4.3 ± 0.3 mm (n = 5); maximum diameter of shield region 31 µm, minimum diameter about 9 µm.

Description of whole mounts: Hair margins at base strongly serrated with simple medulla (A, B), further distally uniserial ladder (C-E), with regular (D) or slightly oval rungs (E), ending in a thin transparent distal hair tip (F).

Form of scale margins: Smooth at base (I, J), dentate (K-M), smooth (N), crenate (O) and smooth (P) at distal hair tip.

Distance between scale margins: Scale margins near (basal part of I) at base, distant (distal part of I-M), near (N) and close (O, P) at distal hair tip.

Cuticular scale patterns: At base simple coronal (I, J), further distally narrow diamond petal (K, L), diamond petal/transitional (M), cupped (N), irregular waves (O) and coronal (P) at distal hair tip.

Description of cross sections: Cross sections predominantly rectangular shaped in outline with emarginations of the long sides and prominent extensions of short sides (Ga) or dumb-bell shaped with rounded short sides (Gb); other cross sections with emarginations of all sides resulting in "star"-like shapes (Gc); all cross sections with medium size or large medulla, sometimes emarginated, reflecting the shape of the cross section; medulla black or grey, cortex brown, light or dark grey.

Crocidura mariquensis (A. Smith, 1844) Swamp musk shrew (Pl. 14)

Origin of hair sample: NKW 16: Punda, KNP, South Africa.

Hair colour: Dorsal and lateral hairs dark grey, ventral hairs brownish-dark grey at basal part and dark brown distally.

Hair types, shape and length: Heavy overhairs straight and without constrictions; curled overhairs (shield hairs) with thickened and grooved distal part and three constrictions; underhairs thinner and undulating at constrictions. Length of overhairs about 6.0 ± 0.6 mm ($n = 7$); maximum diameter of shield region 31 µm, minimum diameter about 7 µm.

Description of whole mounts: Hairs at base with simple medulla (A) and uniserial ladder (B-E), further distally with individual rungs touching one another (D, E), ending in a thin transparent distal hair tip (F).

Form of scale margins: Smooth at base (H, I), dentate (J, K), smooth (L), rippled (M), crenate (N) and smooth (O) at distal hair tip.

Distance between scale margins: Scale margins near (basal part of H) at base, distant (distal part of H-L), near (M) and close (N, O) at distal hair tip.

Cuticular scale patterns: At base simple coronal (H, I), further distally narrow diamond petal (J, K), transitional (basal part of L), cupped (distal part of L), irregular waves (M, N) and coronal (O) at distal hair tip.

Description of cross sections: Cross sections predominantly trapezoidal (Ga), others square in outline with emarginations of all sides resulting in "star"-like shapes (Gb) or circular in outline (Gc); all cross sections with medium size or large medulla, sometimes emarginated, reflecting the shape of the cross section; medulla black or grey, cortex brown, light or dark grey.

Crocidura olivieri martiensseni (Lesson, 1827) Olivier's shrew (Pl. 15)

Origin of hair sample: TM 1026: Mamba, Tanzania (*Sorex martiensseni*).

Hair colour: Hairs dark grey at basal part and dark brown distally.

Hair types, shape and length: Heavy overhairs straight and without constrictions; curled overhairs (shield hairs) with thickened and grooved distal part and three constrictions; underhairs thinner and undulating at constrictions. Length of overhairs about 9.5 ± 0.6 mm ($n = 3$); maximum diameter of shield region 67 µm, minimum diameter about 12 µm.

Description of whole mounts: Hairs at base with simple medulla (A, B), uniserial ladder (C-F) with rungs very close to one another (C) and further distally with irregular rungs forming 'letters' (D), ending in a thin transparent distal hair tip (F).

Form of scale margins: Smooth at base (I, basal part of J), dentate (distal part of J-L), smooth/crenate (M-P) at distal hair tip.

Distance between scale margins: Scale margins near (basal part of I) at base, distant (distal part of I-L), near (M) and close (N-P) at distal hair tip.

Cuticular scale patterns: At base simple coronal (I, basal part of J), narrow diamond petal (distal part of J-K), diamond petal/transitional (L), irregular waves (M), cupped (N), regular waves (O) and coronal (P) at distal hair tip.

Description of cross sections: Cross sections square in outline and emarginations of short sides (Ha), oval (Hb), trapezoidal with (Ga) or without emarginations of the sides (Gb) or circular in outline (Qa); cross sections with small, medium size or large medulla, sometimes emarginated, reflecting the shape of the cross section;

medulla black or grey, cortex brown, light or dark grey, sometimes with a brilliant sheen in transmitted light of microscope (Q).

Crocidura olivieri occidentalis (Lesson, 1827) Olivier's shrew (Pl. 16)

Origin of hair sample: TM 11413: Inyanga, Zimbabwe.

Hair colour: Hairs grey at basal part and brownish-grey distally.

Hair types, shape and length: Heavy overhairs straight and without constrictions; curled overhairs (shield hairs) with thickened and grooved distal part and one or two constrictions; underhairs thinner and undulating at constrictions. Length of overhairs about 5.3 ± 0.1 mm (n = 5); maximum diameter of shield region 38 µm, minimum diameter about 7 µm.

Description of whole mounts: Hairs lack medulla at base (basal part of A), further distally simple medulla (distal part of A), uniserial ladder (B-D), sometimes with irregular rungs forming "letters" (C), distally with oblique rungs (D), ending in a thin transparent distal hair tip (E).

Form of scale margins: Smooth at base (G, H), dentate (I), smooth (J), crenate (K) and smooth (L) at distal hair tip.

Distance between scale margins: Scale margins near (basal part of G) at base, distant (distal part of G-I), near (J) and close (K, L) at distal hair tip.

Cuticular scale patterns: At base simple coronal (G, H), narrow diamond petal (I), diamond petal/transitional, cupped (J), irregular waves (K) and coronal (L) at distal hair tip.

Description of cross sections: Cross section rectangular (Fa) or trapezoidal (Fb) in outline, with emarginations of long sides and small extensions or circular outlines (Fc) of cross sections; all cross sections with small size, sometimes emarginated, reflecting the shape of the cross section; medulla black, brown or grey, cortex brown, light or dark grey.

Crocidura silacea Thomas, 1895 Peters' or lesser grey-brown musk shrew (Pl. 17)

Origin of hair sample: KNP 13482: Skukuza Camp, KNP, South Africa.

Hair colour: Dorsal hairs brownish-grey and dorsal hairs light grey with a brown hue.

Hair types, shape and length: Heavy overhairs straight and without constrictions; curled overhairs (shield hairs) with thickened and grooved distal part and one or two constrictions; underhairs thinner and undulating at constrictions. Length of overhairs about 4.3 ± 0.4 mm (n = 7); maximum diameter of shield region 34 µm, minimum diameter about 8 µm.

Description of whole mounts: Hairs lack medulla at base (basal part of A), further distally simple medulla (distal part of A), uniserial ladder (B-F) with regular rungs, ending in a thin transparent distal hair tip (F).

Form of scale margins: Smooth at base (H), dentate (I-K), smooth (L, M), crenate (N) and smooth (O) at distal hair tip.

Distance between scale margins: Scale margins near (basal part of H) at base, distant (distal part of H-K), near (L, M) and close (N, O) at distal hair tip.

Cuticular scale patterns: At base simple coronal (H), narrow diamond petal (I, J), diamond petal/transitional (K), cupped (L, M), irregular waves (N) and coronal (O) at distal hair tip.

Description of cross sections: Cross sections square (Ga) or trapezoidal (Pa) in outline with emarginations of sides, small extensions and medium size medulla, other cross sections circular in outline with large medulla (Gb); medulla black or grey, cortex brown, light or dark grey.

Crocidura turba Dollman, 1910 Tumultuous shrew (Pl. 18)

Origin of hair sample: TM 13797: N. R. Abercorn, L. Chiela, Zambia.

Hair colour: Hairs dark grey at basal part and brownish-grey distally.

Hair types, shape and length: Heavy overhairs straight and without constrictions; curled overhairs (shield hairs) with thickened and grooved distal part and two or three constrictions; underhairs thinner and undulating at constrictions. Length of overhairs about 6.2 ± 0.5 mm (n = 4); maximum diameter of shield region 36 µm, minimum diameter about 6 µm.

Description of whole mounts: Hairs at base with simple medulla (A, B), further distally uniserial ladder (C-E), at distal part with irregular rungs forming "letters" (D) or "mushroom"-like (E) rungs, ending in a thin transparent distal hair tip (F).

Form of scale margins: Smooth at base (H-J), dentate (K, L), smooth (M), crenate (N, O) and smooth (P) at distal hair tip.

Distance between scale margins: Scale margins near (basal part of H) at base, distant (distal part of H-L), near (M) and close (N-P) at distal hair tip.

Cuticular scale patterns: At base simple coronal (H-J), narrow diamond petal (K), diamond petal/transitional (L), cupped (M), irregular waves (N, O) and coronal (P) at distal hair tip.

Description of cross sections: Cross sections predominantly square (Ga), rectangular, dumb-bell shaped (Gb) or trapezoidal (Gc) in outline with emarginations of long sides and occasionally with small extensions, some with oval outline (Gd); cross sections with small or medium size medulla, sometimes emarginated, reflecting the shape of the cross section; medulla black or grey, cortex brown, light or dark grey, sometimes with a brilliant sheen in transmitted light of microscope.

Myosorex cafer (Sundevall, 1846) Dark-footed forest shrew (Pl. 19)

Origin of hair sample: TM 823: Port St. Johns, Pondoland, Cape Province, South Africa.

Hair colour: Hairs dark grey at basal part and light brown to dark brown distally.

Hair types, shape and length: Heavy overhairs straight and without constrictions; curled overhairs (shield hairs) with thickened and grooved distal part and three constrictions; underhairs thinner and undulating at constrictions. Length of overhairs about 8.3 ± 0.2 mm ($n = 5$); maximum diameter of shield region 40 µm, minimum diameter about 12 µm.

Description of whole mounts: Hairs lack medulla at base (basal part of A), further distally fragmental medulla (distal part of A) and uniserial ladder (B-F), at distal part sometimes with irregular rungs (D), ending in a thin transparent distal hair tip (F).

Form of scale margins: Smooth at base (H, I), dentate (J, K, basal part of L), smooth (distal part of L, basal part of M), crenate/rippled (distal part of M, basal part of N) and coronal (distal part of N) at distal hair tip.

Distance between scale margins: At base scale margins near (basal part of H), distant (distal part of H-L), near (M) and close (N) at distal hair tip.

Cuticular scale patterns: At base simple coronal (H, I), narrow diamond petal (J, K), diamond petal/transitional (basal part of L), cupped (distal part of L, basal part of M) and irregular waves (distal part of M, N) at distal hair tip.

Description of cross sections: Cross sections predominantly square in outline with emarginations of two sides, some with extensions forming the letter "H" (Ga, Oa), some cross sections circular (Gb, Ob) in outline, all cross sections with medium size or large medulla reflecting the shape of the cross section; medulla black, dark or light grey, cortex black, brown or grey, sometimes with a brilliant sheen in transmitted light of microscope (Ga).

Myosorex longicaudatus Meester & Dippenaar, 1978 Long-tailed forest shrew (Pl. 20)

Origin of hair sample: TM 32182: Langeberge, Boosmanskos Wilderness Area, Cape Province, South Africa.

Hair colour: Hairs dark grey at basal part and brownish grey to light brown distally.

Hair types, shape and length: Heavy overhairs straight and without constrictions; curled overhairs (shield hairs) with thickened and grooved distal part and five constrictions; underhairs thinner and undulating at constrictions. Length of overhairs about 8.9 ± 0.4 mm ($n = 6$); maximum diameter of shield region 31 µm, minimum diameter about 5 µm.

Description of whole mounts: Hairs lack medulla at base (basal part of A), further distally simple medulla (distal part of A) and uniserial ladder (B-D), at distal part with regular rungs (C, D), ending in a thin transparent distal hair tip (E).

Form of scale margins: Smooth at base (G), dentate (H, I), smooth (J, K), and rippled (L, M) at distal hair tip.

Distance between scale margins: Scale margins near (basal part of G) at base, distant (distal part of G-J), near (K) and close (L, M) at distal hair tip.

Cuticular scale patterns: At base simple coronal (G), narrow diamond petal (H, I), diamond petal/transitional (J), cupped (K) and irregular waves (L, M) at distal hair tip.

Description of cross sections: Cross sections predominantly square (Fa), occasionally trapezoidal (Fb) in outline with slight emarginations of short sides, some with extensions forming the letter "H", some cross sections circular in outline, medulla of all cross sections small or medium size; medulla black or grey, cortex brown or grey, sometimes with a brilliant sheen in transmitted light of microscope.

Myosorex sclateri Thomas & Schwann, 1905 Sclater's forest shrew (Pl. 21)

Origin of hair sample: TM 32418: Umlalazi Natl. Res. Mtunzini, Natal, South Africa.

Hair colour: Hairs dark grey at basal part and brownish grey to light brown distally.

Hair types, shape and length: Heavy overhairs straight and without constrictions; curled overhairs (shield hairs) with thickened and grooved distal part and five constrictions; underhairs thinner and undulating at constrictions. Length of overhairs about 7.3 ± 0.3 mm (n = 5); maximum diameter of shield region 42 µm, minimum diameter about 9 µm.

Description of whole mounts: Hairs lack medulla at base (basal part of A), further distally simple medulla (distal part of A), uniserial ladder with regular rungs (B-E), ending in a thin transparent distal hair tip (F).

Form of scale margins: Smooth at base (H, I), dentate (J, K), smooth (L), crenate (M) and smooth (N) at distal hair tip.

Distance between scale margins: Scale margins near (basal part of H) at base, distant (distal part of H-K), near (L) and close (M, N) at distal hair tip.

Cuticular scale patterns: At base simple coronal (H, I), narrow diamond petal (J), diamond petal/transitional (K), cupped (L), irregular waves (M) and coronal (N) at distal hair tip.

Description of cross sections: Cross sections predominantly square (Ga), rectangular (Gb) and trapezoidal (Gc) in outline with slight emarginations of short sides, some with extensions forming the letter "H", some cross sections circular (Gd, Oa) in outline, medulla of all cross sections small or medium size; medulla black or grey, cortex black, brown or grey.

Myosorex tenuis Thomas & Schwann, 1905 Zuurbon forest or thin mouse shrew (Pl. 22)

Origin of hair sample: TM 43410: Wolkberg Wilderness Area, Transvaal, South Africa.

Hair colour: Hairs dark grey at basal part and brownish grey to light brown distally.

Hair types, shape and length: Heavy overhairs straight and without constrictions; curled overhairs (shield hairs) with thickened and grooved distal part and five constrictions; underhairs thinner and undulating at constrictions. Length of overhairs about 8.2 ± 0.4 mm (n = 4); maximum diameter of shield region 33 µm, minimum diameter about 9 µm.

Description of whole mounts: Hairs lack medulla at base (basal part of A), further distally simple medulla (distal part of A), uniserial ladder with regular rungs (B, C), ending in a thin transparent distal hair tip (D).

Form of scale margins: Smooth at base (F, G), dentate (H, basal part of I), smooth (distal part of I, J), rippled (K, L) and smooth (M) at distal hair tip.

Distance between scale margins: Scale margins near (basal part of F) at base, distant (distal part of F, G-I), near (J) and close (K-M) at distal hair tip.

Cuticular scale patterns: At base simple coronal (F), narrow diamond petal (G, H), diamond petal/transitional (I), cupped (J), irregular waves (K, L) and coronal (M) at distal hair tip.

Description of cross sections: Cross sections predominantly rectangular (Na), some quadrangular (Ea) in outline with slight emarginations of two or all four sides, some cross sections circular in outline (Eb); medulla medium size or large, sometimes divided (Na) reflecting the shape of the cross section; medulla black or grey, cortex brown or grey, sometimes with a brilliant sheen in transmitted light of microscope (Eb).

Myosorex varius (Smuts, 1832) Forest shrew (Pl. 23)

Origin of hair sample: TM 29409: Cathedral Peak Forest Reserve, Natal, South Africa.

Hair colour: Hairs dark grey at basal part and light brown at distal hair tip.

Hair types, shape and length: Heavy overhairs straight and without constrictions; curled overhairs (shield hairs) with thickened and grooved distal part and six constrictions; underhairs thinner and undulating at constrictions. Length of overhairs about 7.3 ± 0.9 mm (n = 6); maximum diameter of shield region 38 µm, minimum diameter about 6 µm.

Description of whole mounts: Hairs lack medulla at base (basal part of A), further distally simple medulla (distal part of A), uniserial ladder with regular rungs (B-D), ending in a thin distal hair tip (E).

Form of scale margins: Smooth at base (G, H, basal part of I), dentate (distal part of I, J, basal part of K), smooth (distal part of K, L), crenate (M) and smooth (N) at distal hair tip.

Distance between scale margins: Scale margins near (basal part of G) at base, distant (distal part of G-K), near (L) and close (M, N) at distal hair tip.

Cuticular scale patterns: At base simple coronal (G-I), narrow diamond petal (J), diamond petal/transitional (K), cupped (L), irregular waves (M) and coronal (N) at distal hair tip.

Description of cross sections: Cross sections predominantly rectangular (Fa), some quadrangular (Fb) in outline with slight emarginations of short sides and extensions forming the letter "H", some cross sections circular in outline (Fc); all cross sections with small to medium size medulla; medulla black or grey, cortex brown or grey, sometimes with a brilliant sheen in transmitted light of microscope (Fa, b).

Suncus infinitesimus (Heller, 1912) Least dwarf shrew (Pl. 24)

Origin of hair sample: TM 3494: Waterkloof, Pretoria, TV, South Africa.

Hair colour: Hairs dark grey to brownish-grey.

Hair types, shape and length: Heavy overhairs straight and without constrictions; curled overhairs (shield hairs) with thickened and grooved distal part and two constrictions; underhairs thinner and undulating at constrictions. Length of overhairs about 2.7 ± 0.2 mm (n = 7); maximum diameter of shield region 29 µm, minimum diameter about 4 µm.

Description of whole mounts: Hairs lack medulla at base (A); further distally simple medulla (B), uniserial ladder with regular rungs (C, D), ending in a thin transparent distal hair tip (E).

Form of scale margins: Smooth at base (G, basal part of H), dentate (distal part of H, I), smooth (J) and crenate (K-M) at distal hair tip.

Distance between scale margins: Scale margins near (basal part of G) at base, distant (distal part of G-I), near (J, basal part of K) and close (distal part of K-M) at distal hair tip.

Cuticular scale patterns: At base simple coronal (G), narrow diamond petal (H, I), diamond petal/transitional (basal part of J), cupped (distal part of J) and irregular waves (K-M) at distal hair tip.

Description of cross sections: Cross sections predominantly rectangular (Fa), some quadrangular (Fb) in outline with slight emarginations of short sides and with extensions, some cross sections circular in outline (Fc); all cross sections with small to medium size medulla, sometimes divided (Fa) and reflecting the shape of the cross section; medulla black or grey, cortex brown or grey.

Suncus lixus (Thomas, 1898) Greater dwarf shrew (Pl. 25)

Origin of hair sample: TM 41827: Pietermaritzburg Natal, South Africa.

Hair colour: Hairs light grey to dark grey.

Hair types, shape and length: Heavy overhairs straight and without constrictions; curled overhairs (shield hairs) with thickened and grooved distal part and two or three constrictions; underhairs thinner and undulating at constrictions. Length of overhairs about 3.7 ± 0.3 mm (n = 7); maximum diameter of shield region 24 µm, minimum diameter about 7 µm.

Description of whole mounts: Hairs lack medulla at base (basal part of A), further distally simple medulla (distal part of A, B), uniserial ladder (C-F), at distal part with regular (D), oval-shaped (E) or "mushroom"-shaped rungs (F), ending in a thin transparent distal hair tip (G).

Form of scale margins: Smooth at base (I, J) and dentate (K, L) and smooth (M-P) at distal part.

Distance between scale margins: Scale margins near (basal part of I) at base, distant (distal part of I-M), near (N, O) and close (P) at distal end.

Cuticular scale patterns: At base simple coronal (I, J), narrow diamond petal (K), diamond petal (L), transitional (M), cupped (N, O) and coronal (P) at distal end.

Description of cross sections: Cross sections predominantly rectangular (Ha), some trapezoidal (Hb) in outline with slight emarginations of long sides and convex short sides; some cross sections circular in outline (Hc); all cross sections with medium size medulla, reflecting the shape of the cross section; medulla black, cortex lighter brown or grey.

Suncus varilla (Thomas, 1895) Lesser dwarf shrew (Pl. 26)

Origin of hair sample: TM 7842: Odendals Rest, OFS, SA, South Africa.

Hair colour: Hairs dark grey at basal part and light brown distally.

Hair types, shape and length: Heavy overhairs straight and without constrictions; curled overhairs (shield hairs) with thickened and grooved distal part and three constrictions; underhairs thinner and undulating at constrictions. Length of overhairs about 5.5 ± 0.8 mm (n = 7); maximum diameter of shield region 27 µm, minimum diameter about 7 µm.

Description of whole mounts: Hairs lack medulla at base (basal part of A), further distally simple medulla (distal part of A, B), uniserial ladder with regular rungs (C-E), ending in a thin transparent distal hair tip (E).

Form of scale margins: Smooth at base (G, H), dentate (I, J, basal part of K), smooth (distal part of K, L) and crenate (M, N) at distal hair tip.

Distance between scale margins: Scale margins near (basal part of G) at base, distant (distal part of G-K), near (L) and close (M, N) at distal hair tip.

Cuticular scale patterns: At base simple coronal (G, H), narrow diamond petal (I, J), diamond petal/transitional (K), cupped (L) and irregular waves (M, N) at distal hair tip.

Description of cross sections: Cross sections predominantly rectangular (Fa) in outline with slight emarginations of long sides; some cross sections circular (Fb) or oval/oblong (Fc) in outline; all cross sections with small to medium size medulla, reflecting the shape of the cross section; medulla black, cortex lighter brown or grey.

Sylvisorex megalura (Jentink, 1888) Climbing shrew (Pl. 27)

Origin of hair sample: TM 34610: Mount Selinda. Chirinda Forest, Zimbabwe.

Hair colour: Dorsal and lateral hairs dark brown at basal part and dark brown to brownish-grey distally; ventral hairs light grey at basal part and dark brown to brownish-grey distally.

Hair types, shape and length: Heavy overhairs straight and without constrictions; curled overhairs (shield hairs) with thickened and grooved distal part and three constrictions; underhairs thinner and undulating at constrictions. Length of overhairs about 7.3 ± 0.4 mm (n = 7); maximum diameter of shield region 32 µm, minimum diameter about 6 µm.

Description of whole mounts: Hairs lack medulla at base (basal part of A), further distally simple medulla (distal part of A, B), uniserial ladder (C, D), distally sometimes with oblique rungs (D), ending in a thin transparent distal hair tip (E).

Form of scale margins: Smooth at base (G, H), dentate (I, basal part of J), smooth (distal part of J, K), crenate (L) and smooth (M) at distal hair tip.

Distance between scale margins: Scale margins near (basal part of G) at base, distant (distal part of G-J), near (K) and close (L, M) at distal hair tip.

Cuticular scale patterns: At base simple coronal (G, H), narrow diamond petal (I); diamond petal/transitional (J), cupped (K), irregular waves (L) and coronal (M) at distal hair tip.

Description of cross sections: Cross sections predominantly rectangular in outline with emarginations of long sides (Fa), some additionally with one plane short side and extensions on the opposite convex side (Na); some cross sections quadrangular (Fb) and circular (Fc, Nb) in outline; all cross sections with small to large medulla, sometimes divided (Fd) and reflecting the shape of the cross section; medulla black or grey, cortex black, brown or grey, sometimes with a brilliant sheen in transmitted light of microscope (Na, b).

4.3. Order Erinaceomorpha

Family Erinaceidae (hedgehogs)

The pelage of hedgehogs consists of straight, stiff hairs variable in size. Overhairs are relatively long or shorter, very thick and bristle-like (Fig. 1c); underhairs are thinner. Cross sections of hairs are circular, the medulla is simple or of uniserial ladder type. Scale patterns with irregular waves. The described hair characteristics refer to thicker overhairs.

Atelerix frontalis (A. Smith, 1831) Southern African hedgehog (Pl. 28)

Origin of hair sample: TM 8019: Oshikango, Ovamboland, Namibia.

Hair colour: The colour of lateral hairs is dark brown alternating with light brown, hairs of head and some lateral hairs uniformly light brown.

Hair types, shape and length: Length and width of hairs variable from very long and thick to shorter and thinner hairs. Overhairs wider at distal part. Length of overhairs about 24.8 ± 5.9 mm (n = 5); maximum diameter of hair 160 µm, minimum diameter about 29 µm.

Description of whole mounts: Overhairs with black spot and fragmental medulla at base (A), further distally uniserial ladder (B, C) and simple medulla (D-F), distal hair tip transparent (G).

Form of scale margins: At base dentate (I) and crenate (J-N) distally.

Distance between scale margins: Scale margins distant at base (I), near (J-L) and close (M, N) at distal hair tip.

Cuticular scale patterns: At base petal scale patterns (I); irregular waves (J-N) at distal part of hair.

Description of cross sections: Predominantly circular shapes of cross sections with small medulla (Ha) or large medulla (Hc); medulla always dark brown or black, cortex of some cross sections light brown, resulting in an intense brilliant sheen in transmitted light of microscope (Hc), cortex of other sections dark brown or black (Hb)

4.4. Order Chrysochloridea

Family Chrysochloridae (golden moles)

The pelage of golden moles consists of very characteristic soft, silky hairs with a golden sheen. The relatively long overhairs are thicker, grooved and flattened at the distal third and much thinner at their basal part (Fig. 1d). Subtypes of overhairs are shorter and thinner at their distal third. Cross sections of wider part of hairs typically have oval, oblong or concavo-convex outline (Fig. 3); the medulla has wide medulla lattice. Scale patterns of grooved part of shield region always with regular or irregular waves. The described hair characteristics refer to longer and thicker type of overhairs.

Amblysomus hottentotus (A. Smith, 1829) Hottentot golden mole (Pl. 29)

Origin of hair sample: TM 40789: Grasskop Town, Transvaal, South Africa.

Hair colour: Dorsal hairs grey at basal part and distally vary from dark brown to gold; lateral hairs are golden-brown at their distal part; ventral hairs light grey at base and light gold distally.

Hair types, shape and length: Hairs long and very thick at distal third; distal hair tip forming an angle of about 11°. Subtypes distally thinner. Hair length about 13.0 ± 1.3 mm (n = 5); maximum diameter of shield region 153 μm, minimum diameter about 18 μm.

Description of whole mounts: At base fragmental medulla (basal part of A), uniserial ladder (distal part of A), at thicker distal third wide medulla lattice (B-E), occasionally with cells reaching from one margin to the other (D).

Form of scale margins: At base smooth (G, H), dentate (I), smooth (J), rippled (K) and crenate (L) at distal hair tip.

Distance between scale margins: Scale margins near (G, H) at base, distant (I, J); near (K) and close (L) at distal hair tip.

Cuticular scale patterns: At base simple coronal (G, H), club-shaped/transitional (I, J), regular waves (K) and irregular waves (L) at distal hair tip.

Description of cross sections: Cross section of shield region predominantly oblong with medium size or large medulla (Fa), some cross sections with one invaginated convex side (Fb); cross sections of thin basal part of hairs circular in outline with medium size medulla (Fc); medulla always dark brown or black and cortex light brown, resulting in a brilliant sheen in transmitted light of microscope (F).

Amblysomus iris Thomas & Schwann, 1905 Zulu golden mole (Pl. 30)

Origin of hair sample: TM 26304: Diepwalle Forest Res., Krysna, Cape Province, South Africa.

Hair colour: Hairs grey at basal part and greyish-brown distally.

Hair types, shape and length: Hairs relatively short and very thick at distal third; distal hair tip forming an angle of about 4°. Subtypes distally thinner. Hair length about 7.9 ± 0.5 mm (n = 4); maximum diameter of shield region 143 μm, minimum diameter about 14 μm.

Description of whole mounts: At base fragmental medulla (distal part of A), further distally uniserial ladder, at thicker distal third wide medulla lattice (B, C), ending in a transparent thin tip (D).

Form of scale margins: At base smooth scale margins (F), dentate (G, basal part of H), at wider distal third of hair smooth (distal part of H, I-M).

Distance between scale margins: Scale margins close (basal part of F) at base, distant (distal part of F, G-I); near (J) and close (K-M) at distal hair tip.

Cuticular scale patterns: At base simple coronal (F), narrow diamond petal (G, basal part of H), club-shaped/transitional (H, I); regular waves (I-L) and irregular waves (M) at distal hair tip.

Description of cross sections: Cross sections of shield region oblong or concavo-convex in outline with large medulla (Ea); cross section of thin basal portion of hair of circular outline with large medulla (Eb); medulla black and cortex brown or gold, resulting in an intense brilliant sheen in transmitted light of microscope (E).

Calcochloris obtusirostris (Peters, 1851) Yellow golden mole (Pl. 31)

Origin of hair sample: MHN: Tofo, Inhambane Prov., Mozambique; NKW 7: Machai Sandveld, KNP, South Africa.

Hair colour: Hairs yellow-gold at basal part and distally dark brown.

Hair types, shape and length: Hairs relatively short and thick at distal third; distal hair tip forming an angle of about 15°. Subtypes distally thinner. Hair length about 6.3 ± 0.3 mm (n = 5); maximum diameter of shield region 99 μm, minimum diameter about 19 μm.

Description of whole mounts: At base fragmental medulla (basal part of A), further distally uniserial ladder (distal part of A), at thicker distal third wide medulla lattice (B, C), ending in a blunt tip (C).

Form of scale margins: At base with smooth scale margins (E); dentate (F, G); at wider distal third of hair smooth (H) and rippled/crenate (I-K) at distal hair tip.

Distance between scale margins: Scale margins close at base, further distally distant (E-G); at wider distal part of hair near (H, I) and close (J, K) at distal hair tip.

Cuticular scale patterns: At base coronal (basal part of E), further distally narrow diamond petal (F), club-shaped/transitional (G, H) and irregular waves (I-K) at thicker distal third of hair.

Description of cross sections: Cross sections of shield region oblong in outline (Da), slightly dumb-bell shaped (Db) or concavo-convex shapes (Dc) with small medulla; cross section of thin basal part of hair circular in outline with small medulla (Dd); medulla often light brown or grey and cortex dark (Da).

Carpitalpa arendsi Lundholm, 1955 Arend's golden mole (Pl. 32)

Origin of hair sample: TM 12778: Vumba Mt., Umtali Distr., Zimbabwe (*Chlorotalpa arendsi*).

Hair colour: Dorsal and lateral hairs grey at basal part and dark brown further distally. Ventral hairs grey at basal part and distally light brown.

Hair types, shape and length: Hairs relatively long and thick at distal third; distal hair tip forming an angle of about 3°. One subtype with thinner distal part. Hair length about 13.0 ± 0.8 mm (n = 5); maximum diameter of shield region 101 μm, minimum diameter about 5 μm.

Description of whole mounts: At base simple medulla, sometimes fragmental (basal part of A), further distally uniserial ladder (distal part of A); at thicker distal third wide medulla lattice (B-D), ending in a thin tip (E).

Form of scale margins: At base with smooth scale margins (G); dentate (H, basal part of I); at wider distal third of hair smooth (distal part of I, J) and crenate (K-M) at distal hair tip.

Distance between scale margins: Scale margins close at base, further distally distant (G-I); at wider distal part of hair near (J) and close (K-M) at distal hair tip.

Cuticular scale patterns: At base simple coronal (G), further distally narrow diamond petal/composed double chevron (H), club-shaped/transitional (I), regular waves (J) and irregular waves (K-M) at distal hair tip.

Description of cross sections: Cross sections of shield region oblong or oval in outline with large medulla (Fa) or concavo-convex outline with large medulla (Fb); cross section of thin basal part of hair circular in outline with large medulla (Fc); medulla grey or black, cortex of some cross sections light brown resulting in a weak sheen in transmitted light of microscope (Fa), cortex of other sections black.

Chlorotalpa duthieae (Broom, 1907) Duthie's golden mole (Pl. 33)

Origin of hair sample: TM 19119: Krysna, Cape Province, South Africa.

Hair colour: Hairs grey at basal part and brown distally.

Hair types, shape and length: Hairs relatively long and thick at distal third; distal hair tip forming an angle of about 10°. Subtypes with thinner distal part. Hair length about 12.1 ± 1.1 mm (n = 5); maximum diameter of shield region 101 μm, minimum diameter about 7 μm.

Description of whole mounts: At base fragmental medulla (A), further distally uniserial ladder (B); at thicker distal third wide medulla lattice (C-E).

Form of scale margins: Scale margins at base smooth (G), further distally dentate (H); at wider distal third of hair smooth (I), rippled (J) and crenate (K, L) at distal hair tip.

Distance between scale margins: Scale margins near (G) at base, further distally distant (H); at wider distal part of hair near (I, J) and close (K, L) at distal hair tip.

Cuticular scale patterns: At base coronal (G), further distally narrow diamond petal (H), regular waves (I) and irregular waves (J-L) at thicker distal third of hair.

Description of cross sections: Cross sections of shield region oblong with large medulla (Fa) or concavo-convex outline with large medulla (Fb); cross section of thin basal part of hair circular in outline with large medulla; medulla dark grey or black, cortex light brown or grey resulting in a weak sheen in transmitted light of microscope (F).

Chlorotalpa sclateri (Broom, 1907) Sclater's golden mole (Pl. 34)

Origin of hair sample: TM 39445: Mount View, Karoo N. P., Cape Province, South Africa.

Hair colour: Dorsal hairs grey at basal part and brownish-gold distally. Lateral and ventral hairs grey at basal part and light gold at distal part.

Hair types, shape and length: Hairs relatively short and thick at distal third; distal hair tip forming an angle of about 8°. Subtypes with thinner distal part. Hair length about 7.0 ± 0.8 mm (n = 5); maximum diameter of shield region 86 µm, minimum diameter about 10 µm.

Description of whole mounts: At base fragmental medulla (basal part of A), further distally uniserial ladder (distal part of A); at thicker distal third wide medulla lattice (B-D), ending in a thin transparent tip (D).

Form of scale margins: At base smooth (F-H) scale margins, at wider distal third of hair rippled (I) and crenate (J, K) at distal hair tip.

Distance between scale margins: Scale margins near at base (F, G), further distally near (H, I) and close (J, K) at distal hair tip.

Cuticular scale patterns: At base simple coronal (F, basal part of G); at thicker distal third of hair regular waves (H) and irregular waves (I-K).

Description of cross sections: Cross sections of shield region oblong with large medulla (Ea) or concavo-convex outline with large medulla (Eb); cross section of thin basal part of hair circular in outline with large medulla; medulla with brown, grey or black, cortex of some cross sections light brown resulting in an intense brilliant sheen in transmitted light of microscope (E).

Chrysochloris asiatica (Linnaeus, 1758) Cape golden mole (Pl. 35)

Origin of hair sample: TM 5808: Goudini, Worcester, Cape Province, South Africa.

Hair colour: Dorsal hairs grey at basal part and light grey distally; ventral hairs entirely brownish-gold.

Hair types, shape and length: Hairs relatively long and thick at distal third; distal hair tip forming an angle of about 4°. Subtypes shorter and with thinner distal part. Hair length about 11.2 ± 0.5 mm (n = 5); maximum diameter of shield region 92 µm, minimum diameter about 9 µm.

Description of whole mounts: At base uniserial ladder, sometimes fragmental (A); at thicker distal third wide medulla lattice (B, C), ending in a thin transparent tip (C).

Form of scale margins: Scale margins smooth (F-H) at base, at thicker distal third crenate (I-K).

Distance between scale margins: Scale margins near (F-H) at base and close (I-K) at distal hair tip.

Cuticular scale patterns: At base simple coronal (F); at thicker distal third of hair regular waves (G-I) and irregular waves (J, K) at distal hair tip.

Description of cross sections: Cross sections of shield region oblong (Ea) or oval (Eb) with large medulla; cross sections of ventral hairs concavo-convex in outline with medium size medulla (Da); cross section of thin basal part of hair circular in outline with medium size medulla (Db, Ec); medulla black, cortex light brown resulting in an intense brilliant sheen in transmitted light of microscope (D, E).

Chrysospalax trevelyani (Günther, 1875) Giant golden mole (Pl. 36)

Origin of hair sample: TM 746: Port St. Johns, Cape Prov., South Africa.

Hair Colour: Hairs light yellow at basal part and dark brow distally.

Hair types, shape and length: Hairs very long and very thick at distal third; distal hair tip forming an angle of about 9°. Subtypes with thinner distal part. Hair length about 20.6 ± 0.4 mm (n = 5); maximum diameter of shield region 190 µm, minimum diameter about 25 µm.

Description of whole mounts: At base fragmental medulla (A), further distally uniserial ladder (B); at thicker distal third wide medulla lattice (C-E).

Form of scale margins: At base with smooth (G) scale margins, dentate (H, I), smooth (J, K) and crenate (L, M) at distal hair tip.

Distance between scale margins: Scale margins close (G) at base, further distally distant (H-J), near (K) and close (L, M) at distal hair tip.

Cuticular scale patterns: Simple coronal (G) at base, narrow diamond petal (H), club-shaped/transitional (I, J), regular waves (K, L) and irregular waves (M) at distal hair tip.

Description of cross sections: Cross sections of shield region predominantly oblong with large medulla (F); cross section of thin basal part of hair circular in outline with medium size medulla; medulla black, cortex light brown resulting in an intense brilliant sheen in transmitted light of microscope (F).

Chrysospalax villosus (A. Smith, 1833) Rough-haired golden mole (Pl. 37)

Origin of hair sample: TM 22416: Pietermaritzburg Natal, South Africa.

Hair colour: Hairs grey at basal part and dark brow distally.

Hair types, shape and length: Hairs very long and thick at distal third; distal hair tip forming an angle of about 2°. Subtypes with thinner distal part. Hair length about 20.8 ± 1.0 mm (n = 5); maximum diameter of shield region 105 µm, minimum diameter about 11 µm.

Description of whole mounts: At base fragmental simple medulla (A), at distal third of hair wide medulla lattice (B, C); ending in a thin, transparent distal hair tip (D).

Form of scale margins: At base smooth (G) scale margins, dentate (H); at wider distal third of hair smooth (I), smooth/crenate (J), rippled (K) and crenate (L, M) at distal hair tip.

Distance between scale margins: Scale margins near at base (G), further distally distant (H, I), near (J) and close (K-M) at distal part of hair.

Cuticular scale patterns: At base simple coronal (G), narrow diamond petal (H), club-shaped/transitional (I), regular waves (J) and irregular waves (K-M) at distal hair tip.

Description of cross sections: Cross sections of shield region predominantly oblong (Fa) and oval (Ea, Fb) with large medulla; cross section of thin basal part of hair circular in outline with large medulla (Eb); medulla dark grey or black, cortex light brown, resulting in an intense brilliant sheen in transmitted light of microscope (E, F).

Cryptochloris wintoni (Broom, 1907) de Winton's golden mole (Pl. 38)

Origin of hair sample: TM 8235: Port Nolloth, Namaqualand, Cape Prov, South Africa.

Hair colour: Hairs dark grey at basal part and of gold colour distally.

Hair types, shape and length: Hairs relatively short and thick at distal third; distal hair tip forming an angle of about 12°. Subtypes with thinner distal part. Hair length about 6.9 ± 0.6 mm (n = 5); maximum diameter of shield region 113 µm, minimum diameter about 9 µm.

Description of whole mounts: At base fragmental uniserial ladder (A); at thicker distal third wide medulla lattice with large aerial spaces (B-D).

Form of scale margins: At base smooth (F) scale margins, further distally dentate (G); at wider distal third of hair smooth (H) and crenate (I-K) at distal hair tip.

Distance between scale margins: Scale margins close at base (F), further distally distant (G), near (H, I) and close (J, K) at distal hair tip.

Cuticular scale patterns: At base coronal (F), further distally narrow diamond petal (G); at thicker distal third of hair regular waves (H) and irregular waves (I-K) at distal hair tip.

Description of cross sections: Cross sections of shield region predominantly oblong with small medulla (Ea) and some cross sections with one invaginated convex side (Eb); cross section of thin basal part of hair circular in outline with medium size medulla (Ec); medulla light or dark grey, cortex light brown, resulting in an intense brilliant sheen in transmitted light of microscope (E).

Eremitalpa granti (Broom, 1907) Grant's golden mole (Pl. 39)

Origin of hair sample: TM 8237: North Nolloth Distr., Namaqualand, Cape Province, South Africa; TM 15154: Sossusvlei, Namib Desert, Namibia.

Hair colour: Dorsal hairs grey and dark brown at small portion of distal tip, lateral and ventral hairs grey at basal part and distally of light gold colour.

Hair types, shape and length: Hairs long and moderately thick at distal third; distal hair tip forming an angle of about 6°. Subtypes with thinner distal part. Hair length about 15.5 ± 0.6 mm (n = 5); maximum diameter of shield region 78 µm, minimum diameter about 9 µm.

Description of whole mounts: At base fragmental uniserial ladder (A), at thicker distal third wide medulla lattice (B-E) with larger clear spaces (D).

Form of scale margins: Scale margins smooth (G, H) at base, and crenate (I-K) at distal third of hair.

Distance between scale margins: At base scale margins near (G, H) and close (I-K) at distal third of hair.

Cuticular scale patterns: At base simple coronal (basal part of G), regular waves (distal part of G, H); at thicker distal third of hair irregular waves (H-K).

Description of cross sections: Cross sections of shield region predominantly oblong (Fa) or dumb-bell shaped with large medulla (Fb), occasionally concavo-convex in outline; cross section of thin basal part of hair circular in outline with medium size medulla (Fc); medulla light or dark grey, cortex light brown, resulting in a weak sheen in transmitted light of microscope (F).

Neamblysomus gunningi (Broom, 1908) Gunning's golden mole (Pl. 40)

Origin of Hair Sample: TM 40780: Magoebas Kloof, de Hoek Nat. Res. Transvaal, South Africa (*Amblysomus gunningi*).

Hair colour: Dorsal hairs light grey at basal part and distally brown, lateral and ventral hairs light grey at basal part and distally of gold colour.

Hair types, shape and length: Hairs moderately long and thick at distal third; distal hair tip forming an angle of about 6°. Subtypes with thinner distal part. Hair length about 8.1 ± 1.1 mm (n = 4); maximum diameter of shield region 102 µm, minimum diameter about 9 µm.

Description of whole mounts: At base uniserial ladder (A); at thicker distal third wide medulla lattice (B, C), sometimes with clear spaces (B), ending in a thin tip (C).

Form of scale margins: At base smooth (E-G) scale margins and crenate (H, I) at distal hair tip.

Distance between scale margins: At base scale margins near (E-G) and close (H, I) at distal hair tip.

Cuticular scale patterns: At base coronal (basal part of E), club-shaped/transitional (F); at thicker distal third of hair regular waves (H) and irregular waves (H, I) at distal hair tip.

Description of cross sections: Cross sections of shield region predominantly dumb-bell shaped with large medulla (Da); cross section of thin basal part of hair circular in outline with medium size (Db) or small medulla (Dc); medulla black, light or dark grey, cortex dark or light brown, resulting in a brilliant sheen in transmitted light of microscope (D).

Neamblysomus julianae Meester, 1972 Juliana's golden mole (Pl. 41)

Origin of hair sample: NKW 4: Manchulane, KNP, South Africa (=*Amblysomus julianae*).

Hair colour: Hairs grey at basal part and distally light to dark brown.

Hair types, shape and length: Hairs relatively long and thick at distal third; distal hair tip forming an angle of about 7°. Subtypes shorter and with thinner distal part. Hair length about 13.8 ± 0.7 mm (n = 5); maximum diameter of shield region 86 µm, minimum diameter about 14 µm.

Description of whole mounts: At base uniserial ladder (A); at thicker distal third wide medulla lattice (B-D) with some aerial spaces (C), ending in a thin tip (D).

Form of scale margins: At base scale margins smooth (F-J) and crenate/rippled (K-N) at distal hair tip.

Distance between scale margins: At base scale margins near (F, G), further distally distant (H-J), near (K, L) and close (M, N).

Cuticular scale patterns: At base simple coronal (F, G), further distally club-shaped/transitional (H), regular waves (I, J) and irregular waves (K-N) at distal hair tip.

Description of cross sections: Cross sections of shield region oblong (Ea) and dumb-bell shaped (Eb) with large medulla; cross section of thin basal part of hair circular in outline with medium size medulla (Ec); medulla black, light or dark grey, cortex light brown, resulting in an intense brilliant sheen in transmitted light of microscope (E).

5. KEY TO SOUTHERN AFRICAN ELEPHANT-SHREWS, SHREWS, HEDGEHOGS AND GOLDEN MOLES BASED ON HAIR CHARACTERISTICS

1 Pelage composed of distally enlarged overhairs and slightly curved underhairs with or without constrictions (Fig. 1a); hairs occasionally with intumescence (e.g., Pl. 1F & G, 4F, 6F, 7B & F); length of dorsal hairs varies between 11 mm and 18 mm; medulla with uniserial ladder, medulla of some species distally with wide lattice; scale patterns of distal part of hair with regular or irregular waves, hair tip often of coronal type; cross section almost always circular .... **elephant-shrews**

2 Pelage composed of straight, long heavy overhairs without constrictions, a second type of distally enlarged, grooved and slightly curved overhairs (shield hairs) and undulating underhairs (Fig. 1b); the latter two types with one or several constrictions along the hair (Pl. 13 H); hairs very short varying between 3 mm and 10 mm; except from immediate base and tip, medulla always with uniserial ladder; scale patterns of grooved part of shield region always cupped, hair tip with coronal or regular waves; cross section of enlarged part of shield hair typically rectangular, or "H"-like with two or more emarginations (e.g., Pl. 9Gb) .... **shrews**

3 Pelage composed of straight, stiff, distally enlarged overhairs lacking constrictions and dilatations (Fig. 1c) and thinner underhairs; length of hairs up to 25 mm; medulla simple or with uniserial ladder; scale patterns with irregular waves; cross section circular .... **hedgehogs**

4 Pelage composed of long overhairs (shield hairs) with distal third expanded, flattened and club-like (Fig. 1d) and shorter sub-types with thinner distal part; length of dorsal hairs between 6 mm and 21 mm; medulla at thickened part of hair always with wide medulla lattice; scale patterns of grooved part of shield region always with regular or irregular waves; cross section of enlarged part of hair oblong, oval or concavo-convex .... **golden moles**

Elephant-shrews (or sengis)

1a Maximum diameter of hairs between 40 µm and 70 µm 2

1b Maximum diameter of hairs smaller than 40 µm .. 5

2a Cross sections with golden sheen in transmitted light of microscope 3

2b Cross sections not with golden sheen in transmitted light of microscope 4

3a Hair length about 16 mm; wide medulla lattice at distal part of overhair; maximum diameter of hairs approx. 58 µm; circular cross sections with bright sheen. Distribution: N South Africa and NE Namibia; Angola; S Zaire; Zimbabwe, Mozambique to Kenya and Uganda ...***Elephantulus brachyrhynchus***

3b Hair length about 18 mm; medulla with uniserial ladder; maximum diameter of hairs approx. 59 µm; circular cross sections with bright sheen. Distribution: Mozambique; Tanzania (including Mafia and Zanzibar); SE Kenya; S Uganda; Zambia, Malawi; SE Zimbabwe; Zaire; Namibia; NE Angola; N Natal and E Transvaal, South Africa .... ***Petrodromus tetradactylus***

4a Medulla with uniserial ladder; hair length about 15 mm; maximum diameter of hairs approx. 53 µm; cross sections circular in outline. Distribution: SW Angola; Namibia; Botswana; NW Transvaal and N Cape Prov., South Africa .... ***Elephantulus intufi***

4b Hair length about 12 mm; medulla with wide medulla lattice; maximum diameter of hairs approx. 46 µm; cross sections circular in outline. Distribution: Zimbabwe, Namibia, E Botswana, E and N South Africa, Mozambique .... ***Elephantulus myurus***

5a Hair length about 18 mm; medulla with uniserial ladder; maximum diameter of hairs about 34 µm; circular cross sections with bright sheen. Distribution: Namibia; Cape Prov., South Africa .... ***Elephantulus rupestris***

5b Hair length about 14 mm; medulla with uniserial ladder; maximum diameter of hairs approx. 30 µm; circular cross sections without sheen. Distribution: SW and C Cape Prov., South Africa .... ***Elephantulus edwardi***

5c Hair length about 18 mm; medulla with uniserial ladder; maximum diameter of hairs approx. 26 µm; circular cross sections with bright sheen. Distribution: W and NW Cape Prov., South Africa to SW Namibia ....***Macroscelides proboscideus***

Shrews

1a Length of overhairs longer than 7 mm 2

1b Length of overhairs shorter than 7 mm 5

2a Cross sections of widest part of shield hair in the form of an H in outline 3

2b Cross sections of widest part of shield hair not in the form of an H in outline **4**

3a Hair length about 8.3 mm; maximum diameter of hairs about 40 µm. Distribution: South Africa, eastern escarpment and north to the Transvaal; extreme W Mozambique and E Zimbabwe . ***Myosorex cafer***

3b Hair length about 8.9 mm; maximum diameter of hairs about 31 µm. Distribution: SE Cape Province, South Africa .... ***Myosorex longicaudatus***

3c Hair length about 7.3 mm; maximum diameter of hairs about 42 µm; distribution: Natal, South Africa; Swaziland; Mozambique; Zimbabwe .... ***Myosorex sclateri***

3d Hair length about 8.2 mm; maximum diameter of hairs about 33 µm. Distribution: Transvaal, South Africa; possibly W Mozambique .. ***Myosorex tenuis***

3e Hair length about 7.3 mm; maximum diameter of hairs about 38 µm. Distribution: South Africa, from NW Cape Province to E Transvaal; Lesotho and Orange Free State .... ***Myosorex varius***

4a Hair length about 9.5 mm; maximum diameter of hairs about 67 µm; medulla typically with 'letters' (Pl. 15D). Distribution: Egypt; Senegal to Ethiopia and southwards to N South Africa .... ***Crocidura olivieri martiensseni***

4b Hair length about 7.3 mm; maximum diameter of hairs about 32 µm; cross sections quadrangular or rectangular in outline with plane and convex short sides (Pl. 27 Na). Distribution: Upper Guinea to Ethiopia and south to Namibia, Angola, Mozambique and Zimbabwe .... ***Sylvisorex megalura***

5a Hair length shorter than 4 mm **6**

5b Hair length between 4 mm and 7 mm **7**

6a Hair length about 2.7 mm; maximum diameter of hairs about 26 µm; cross sections rectangular in outline with a deep invagination of one side resulting in prominent extensions of the margin (Pl. 10Fa). Distribution: Sudan and Guinea, from Senegal to Ethiopia and south to South Africa .... ***Crocidura fuscomurina***

6b Hair length about 2.7 mm; maximum diameter of hairs about 29 µm. Distribution: South Africa to Kenya; Central African Republic; Cameroon .... ***Suncus infinitesimus***

6c Hair length about 3.7 mm; maximum diameter of hairs about 24 µm. Distribution: Kenya, Tanzania, Malawi, Zaire, Zambia, Angola, Botswana, Namibia, Zimbabwe and Transvaal, South Africa .... ***Suncus lixus***

7a Cross sections dumb-bell shaped in outline; rungs of uniserial ladder irregular and often like "letters" ... **8**

7b Cross sections quadrangular or rectangular in outline; rungs of uniserial ladder more regular **9**

8a Hair length about 5.5 mm; maximum diameter of hairs about 33 µm. Distribution: Angola, Zaire, Uganda, Kenya, Somalia, Tanzania, Malawi, Zimbabwe, Zambia, Mozambique, Botswana, Namibia, South Africa .... ***Crocidura hirta***

8b Hair length about 4.3 mm; maximum diameter of hairs about 31 µm. Distribution: Transvaal, South Africa; Swaziland, Nyamaziwa Falls, Matopo Hills, Zimbabwe .... ***Crocidura maquassiensis***

8c Hair length about 6.7 mm; maximum diameter of hairs about 31 µm. Distribution: Mozambique, Zambia, Zimbabwe, E Angola, Zaire, Malawi, Tanzania, Kenya, Uganda, Rwanda ..... ***Crocidura luna***

8d Hair length about 6.2 mm; maximum diameter of hairs about 36 µm. Distribution: Angola, Zambia, Zaire, Malawi, Tanzania, Kenya, Uganda, Cameroon .... ***Crocidura turba***

8e Hair length about 5.5 mm; maximum diameter of hairs about 35 µm. Distribution: southern and eastern South Africa, southern Mozambique .... ***Crocidura flavescens***

9a Hair length about 6.2 mm; maximum diameter of hairs about 29 µm. Distribution: South Africa, Namibia, Angola, Botswana, Mozambique, records further north uncertain .... ***Crocidura cyanea***

9b Hair length about 5.3 mm; maximum diameter of hairs about 38 µm; medulla typically with "letters" (Pl. 16C). Distribution: Egypt; Senegal to Ethiopia, and southwards to N South Africa .... ***Crocidura olivieri occidentalis***

9c Hair length about 6.0 mm; maximum diameter of hairs about 31 µm. Distribution: South Africa to Mozambique, W Zimbabwe and Zambia; NW Botswana and NE Namibia to SC Angola; perhaps SE Zaire .... ***Crocidura mariquensis***

9d Hair length about 4.3 mm; maximum diameter of hairs about 34 µm. Distribution: most of South Africa, parts of Botswana, Mozambique and Zimbabwe; possibly wider distribution .... ***Crocidura silacea***

9e Hair length about 5.5 mm; maximum diameter of hairs about 27 µm. Distribution: Cape, South Africa to Zimbabwe, Mozambique, Zambia, Tanzania, E Zaire, Malawi; an isolated record from Nigeria .... ***Suncus varilla***

Hedgehogs

1 Hair length about 25 mm; maximum diameter of hairs about 160 µm; overhairs with black spot at base (Pl. 28A). Distribution: Cape Province, South Africa to E Botswana and W Zimbabwe, Namibia to SW Angola, Zambia .... ***Atelerix frontalis***

Golden moles

1a Hair length about 21 mm 2

1b Hair length much less than 21 mm 3

2a Hair length about 21 mm; maximum diameter of hairs about 190 µm; distal hair tip forming an angle of about 9°. Distribution: Cape Prov., South Africa .... ***Chrysospalax trevelyani***

2b Hair length about 21 mm; maximum diameter of hairs about 105 µm; distal hair tip forming an angle of about 2°. Distribution: Transvaal and Natal, South Africa .... ***Chrysospalax villosus***

3a Maximum diameter of hairs between 125 µm and 160 µm 4

3b Maximum diameter of hairs smaller than 125 µm 5

4a Distal hair tip forming an angle of about 11°; hair length about 13 mm; maximum diameter of hairs about 153 µm. Distribution: Natal, Transvaal to S Cape Prov., also NE Orange Free State, South Africa; Lesotho; Swaziland; S Mozambique .... ***Amblysomus hottentotus***

4b Distal hair tip forming an angle of about 4°; hair length about 8 mm; maximum diameter of hairs about 143 µm. Distribution: S Cape Prov. to Transkei, Natal, including Zululand, and SE Transvaal, South Africa; S Mozambique .... ***Amblysomus iris***

5a Distal hair tip forming an angle of about 15°; hair length about 6 mm; maximum diameter of hairs about 99 µm. Distribution: Zululand and E Transvaal, South Africa; S Zimbabwe; S Mozambique .... ***Calcochloris obtusirostris***

5b Distal hair tip forming an angle < 15° 6

6a Medulla lattice with large aerial spaces; hair length about 7 mm; maximum diameter of hairs about 113 µm; distal hair tip forming an angle of about 12°. Distribution: Little Namaqualand; Cape Prov., South Africa .... ***Cryptochloris wintoni***

6b Medulla lattice not with large aerial spaces 7

7a Cross sections of extended part of ventral hairs predominantly showing concavo-convex outline (Pl. 35Da); hair length about 11 mm; maximum diameter of hairs about 92 µm; distal hair tip forming an angle of about 4°. Distribution: W Cape Prov. and Robben Isl., South Africa; perhaps Damaraland, Namibia .... ***Chrysochloris asiatica***

7b Cross sections of extended part of ventral hairs predominantly showing other than concavo-convex outline 8

8 **The following species can be distinguished according to their distribution:**

8a Hair length about 8 mm; maximum diameter of hairs about 102 µm; distal hair tip forming an angle of about 6°. Distribution: E Transvaal, South Africa .... ***Neamblysomus gunningi***

8b Hair length about 14 mm; maximum diameter of hairs about 86 µm; distal hair tip forming an angle of about 7°. Distribution: Pretoria, Nylstroom/Nylsvley and Kruger Nat. Park (Transvaal), South Africa .... ***Neamblysomus julianae***

8c Hair length about 13 mm; maximum diameter of hairs about 101 µm; distal hair tip forming an angle of about 3°. Distribution: E Zimbabwe and adjacent Mozambique .... ***Carpitalpa arendsi***

8d Hair length about 12 mm; maximum diameter of hairs about 101 µm; distal hair tip forming an angle of about 10°. Distribution: S Cape Prov., South Africa .... ***Chlorotalpa duthieae***

8e Hair length about 7 mm; maximum diameter of hairs about 86 µm; distal hair tip forming an angle of about 8°. Distribution: Cape Prov., E Orange Free State, S Transvaal, South Africa; Lesotho .... ***Chlorotalpa sclateri***

8f Hair length about 16 mm; maximum diameter of hairs about 78 µm; distal hair tip forming an angle of about 6°. Distribution: Cape Prov., South Africa to Namib Desert, Namibia; Botswana .... ***Eremitalpa granti***

Acknowledgements. The authors wish to thank the Maputo Natural History Museum, Scientific Services of Kruger National Park and Transvaal Museum, Pretoria for providing hair samples. Further thanks to Dr. Chris Tidemann, Australian National University, Canberra for providing materials; Bembergcell SPA, Milano, Italy for providing cellulose acetate yarn; Mr. Ralf Loeper, University Mainz, Germany, for his support during the initial phase of the study; Mr. Ottmar Fischer, University Freiburg, Germany for the electron microscopy of hair samples; Dr. Esteban Sarmiento, American Natural History Museum, New York and Dr. Rick Bein, University Indiana University Purdue University, Indianapolis, for their critical comments on the manuscript and Centrum für Internationale Migration und Entwicklung (CIM) for funding.

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Received: 26.10.2004
Revided: 02.04.2005
Accepted: 15.05.2006
Corresponding editor: G. Peters

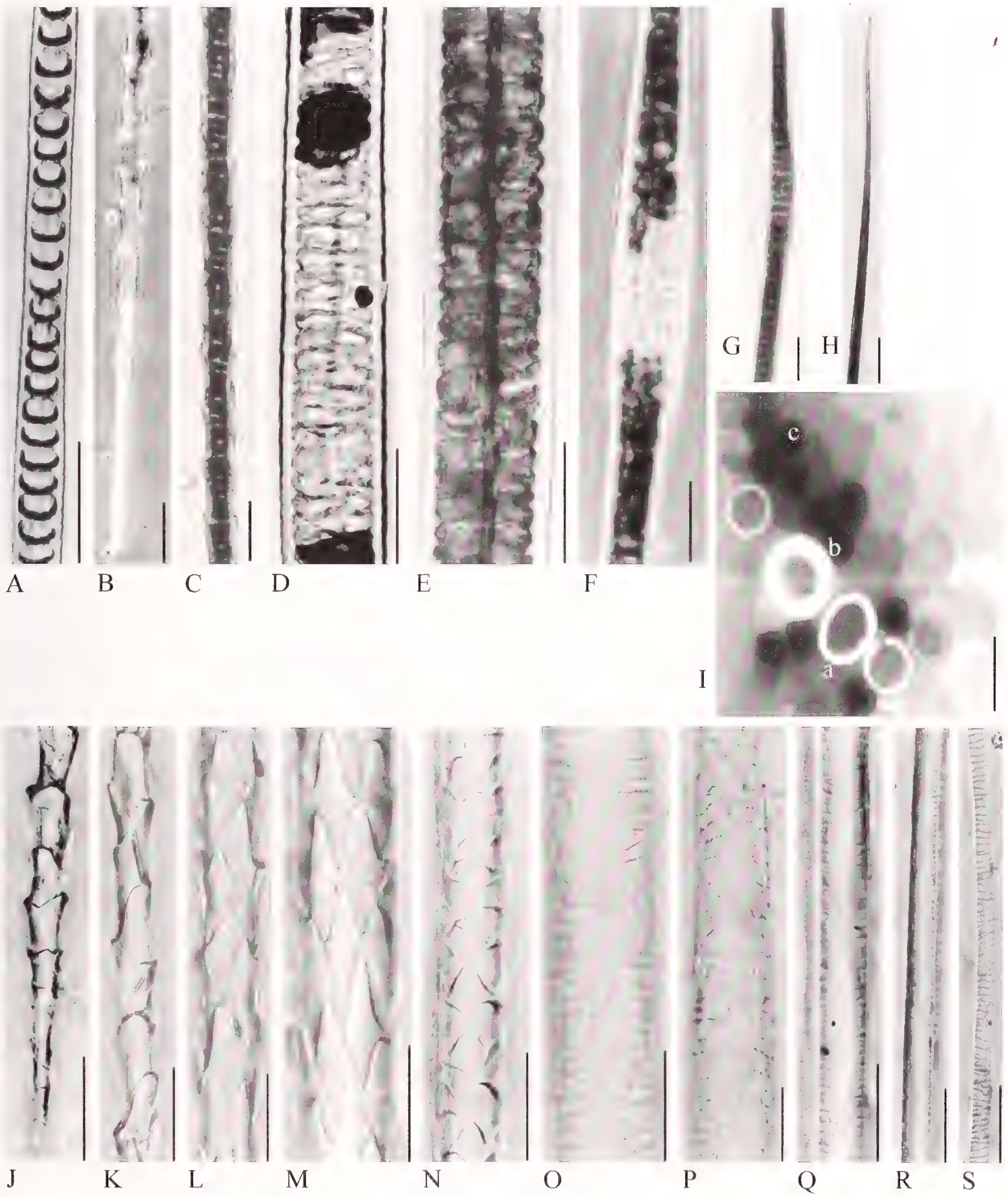
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Plate 1. Whole mounts, cross sections and cuticular scale casts of *Elephantulus brachyrhynchus* (bars equivalent to 50 μm).

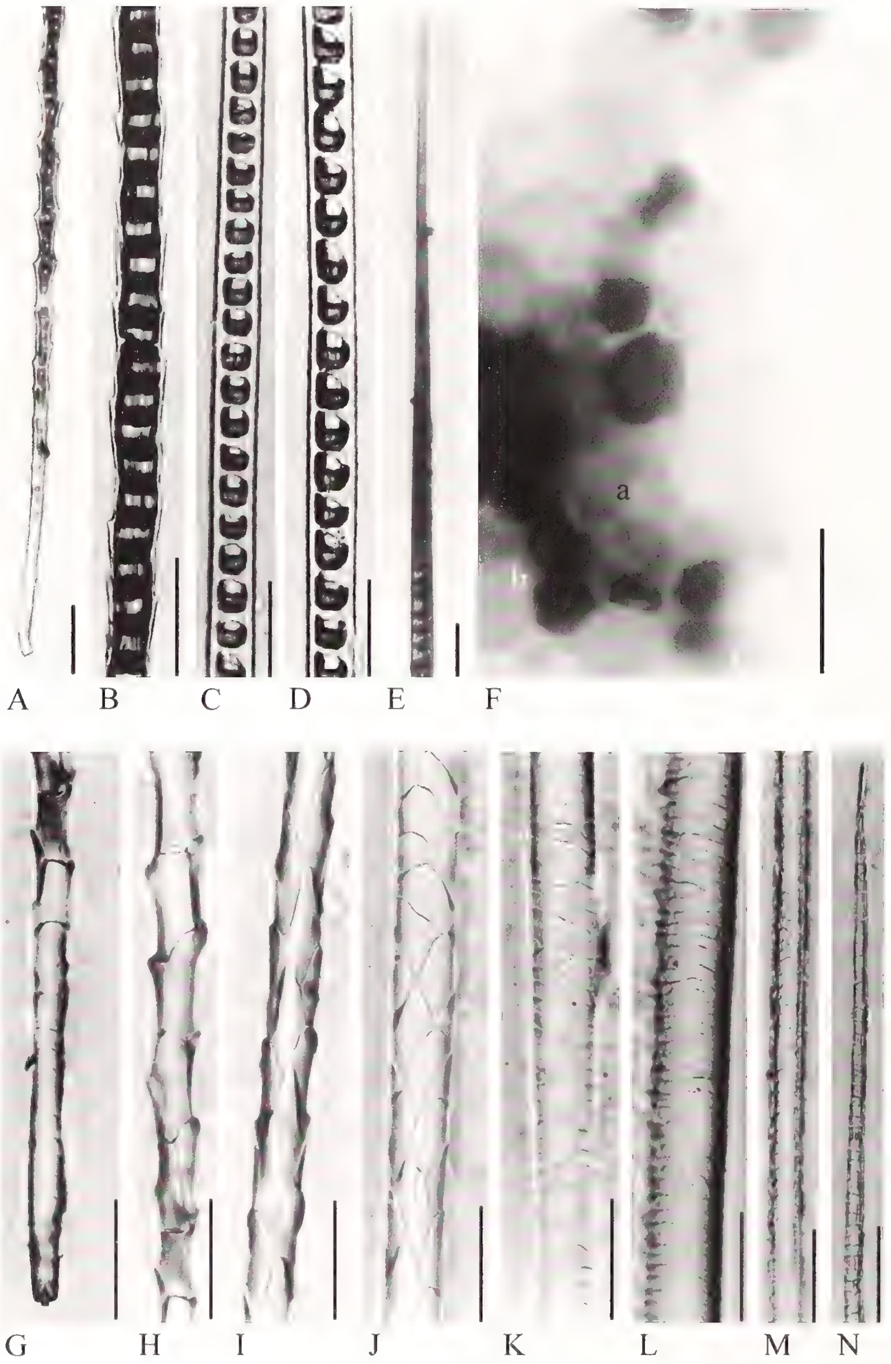
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Plate 2. Whole mounts, cross sections and cuticular scale casts of *Elephantulus edwardi* (bars equivalent to 50 µm).

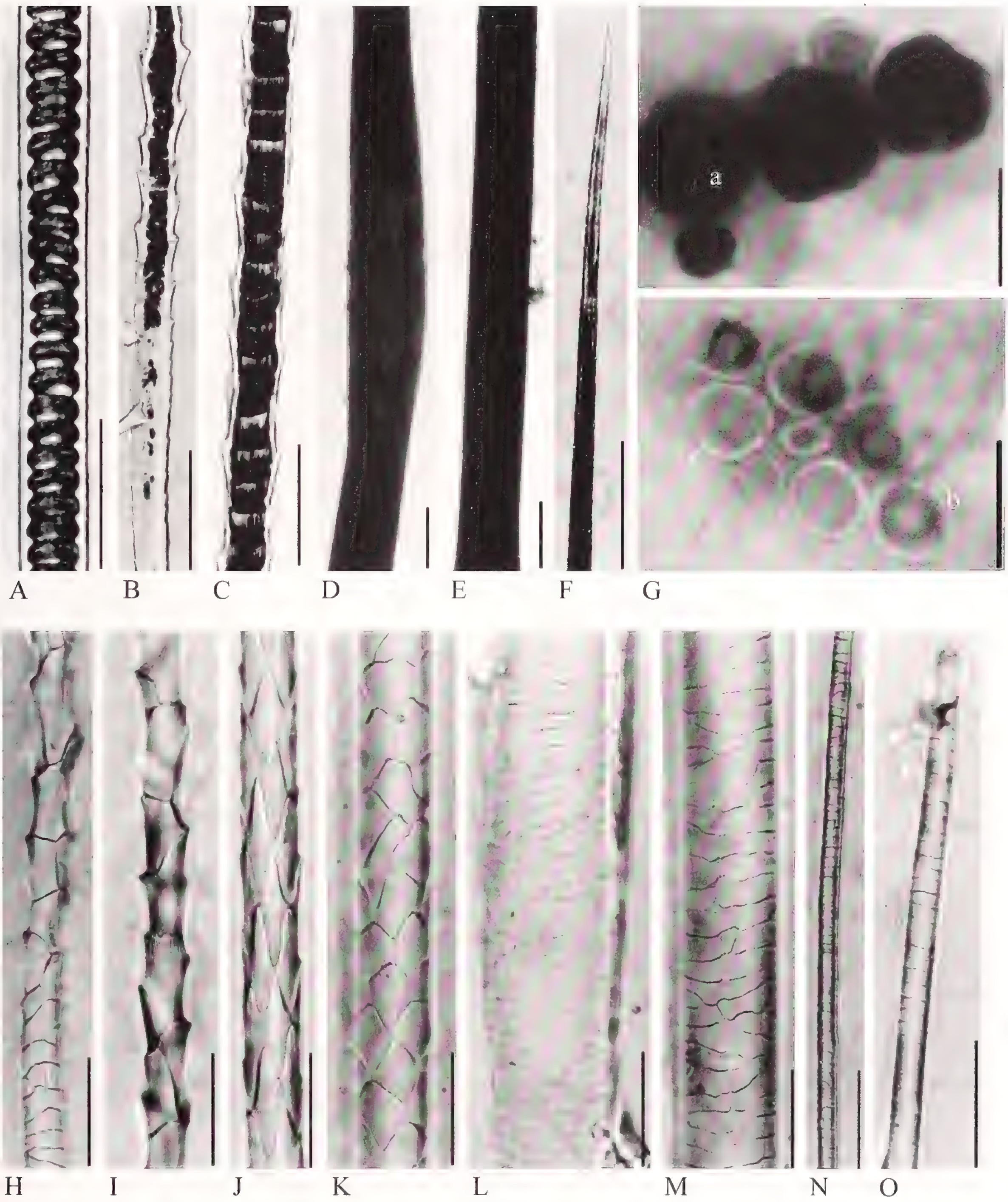
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Plate 3. Whole mounts, cross sections and cuticular scale casts of *Elephantulus intufi* (bars equivalent to 50 μm).

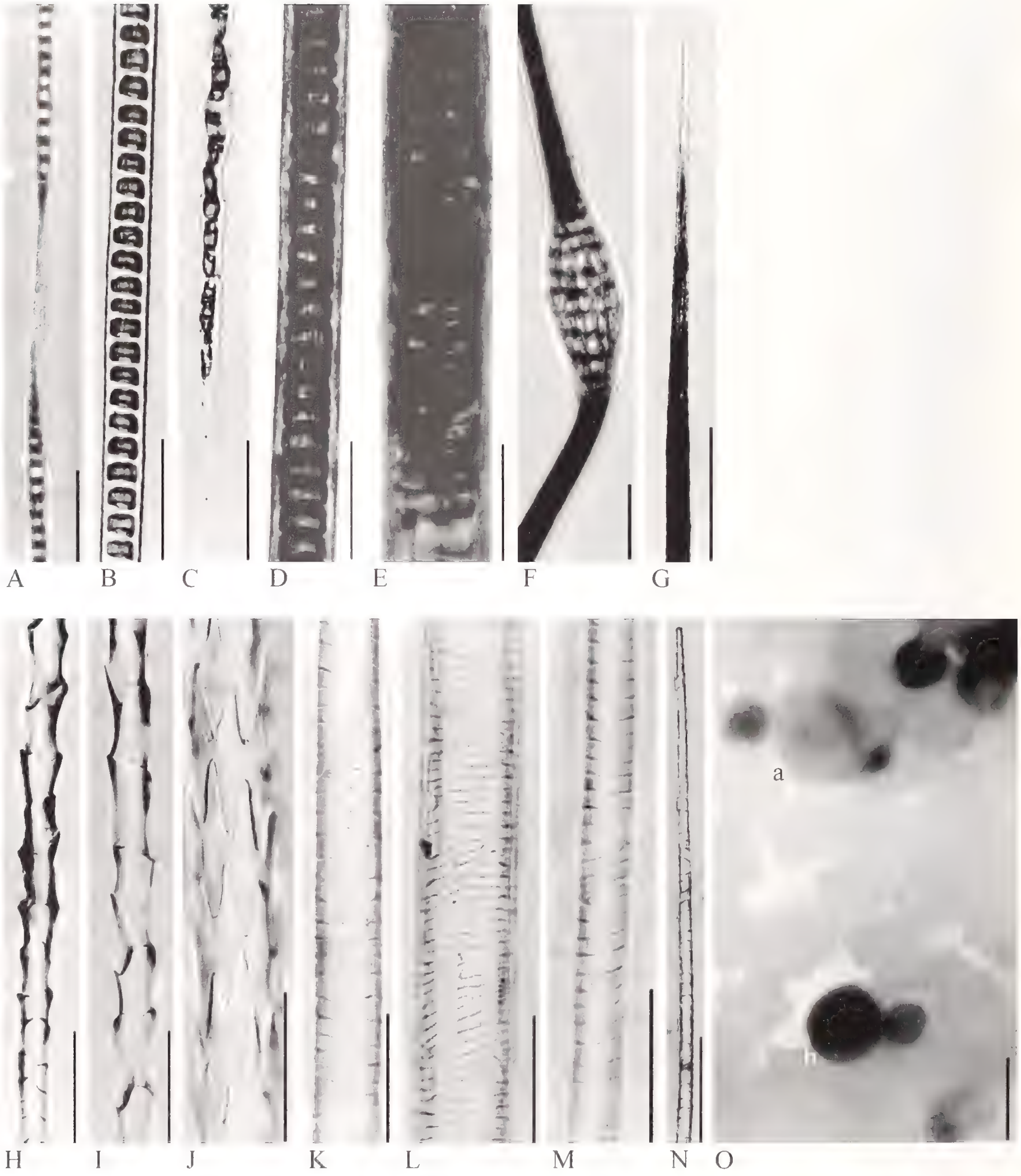
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Plate 4. Whole mounts, cross sections and cuticular scale casts of *Elephantulus myurus* (bars equivalent to 50 µm).

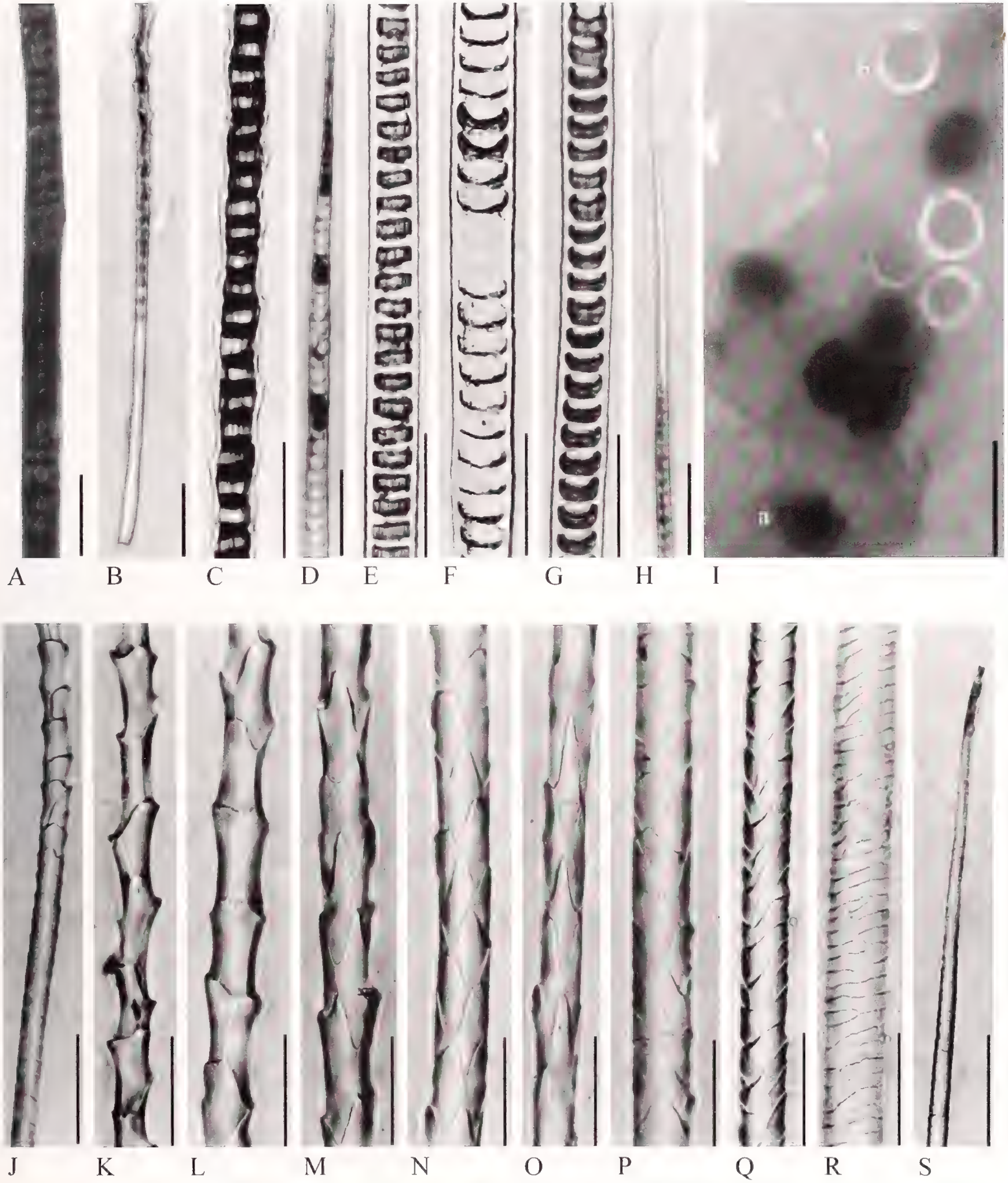
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Plate 5. Whole mounts, cross sections and cuticular scale casts of *Elephantulus rupestris* (bars equivalent to 50 μm).

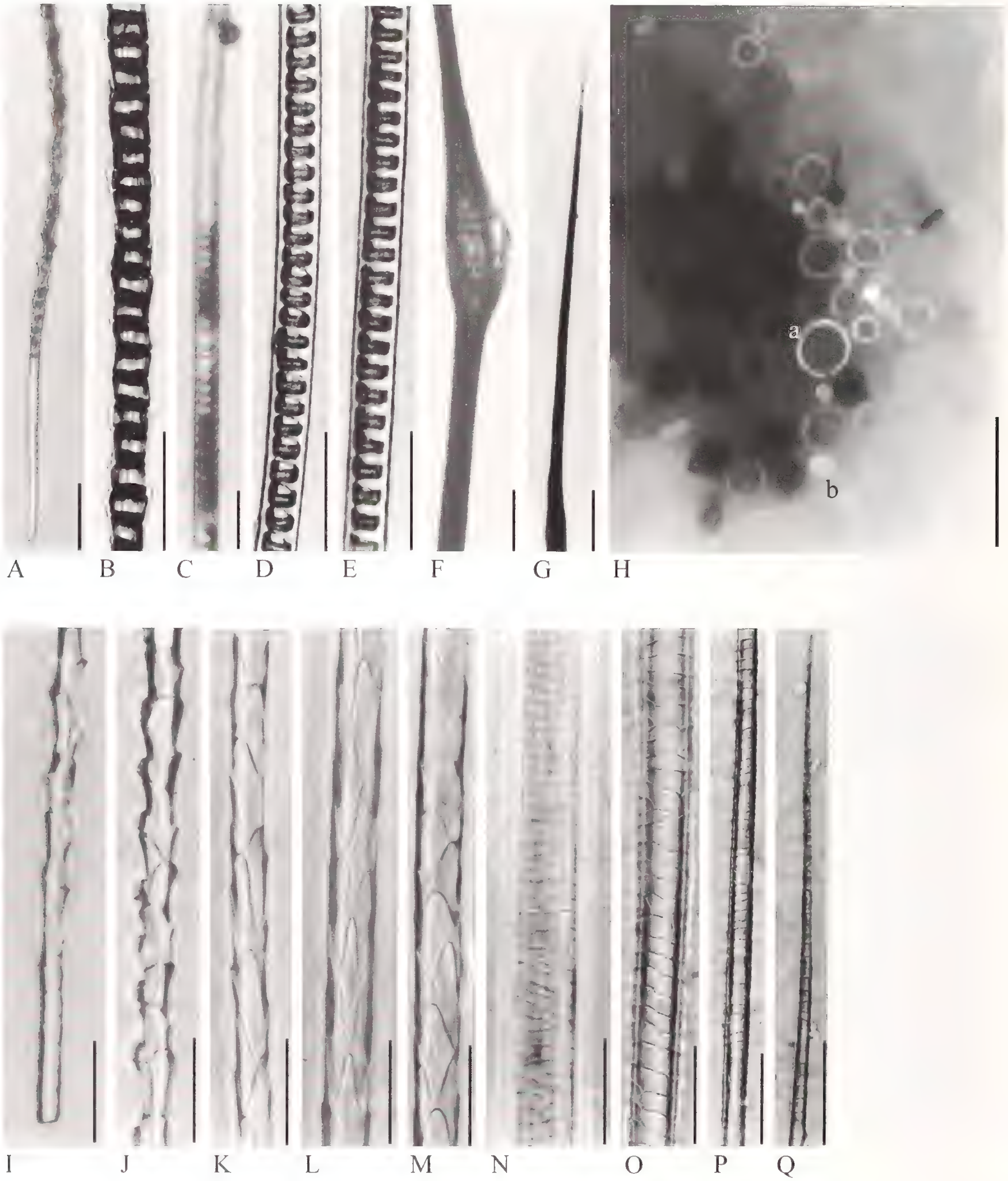
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Plate 6. Whole mounts, cross sections and cuticular scale casts of *Macroscelides proboscideus* (bars equivalent to 50 µm).

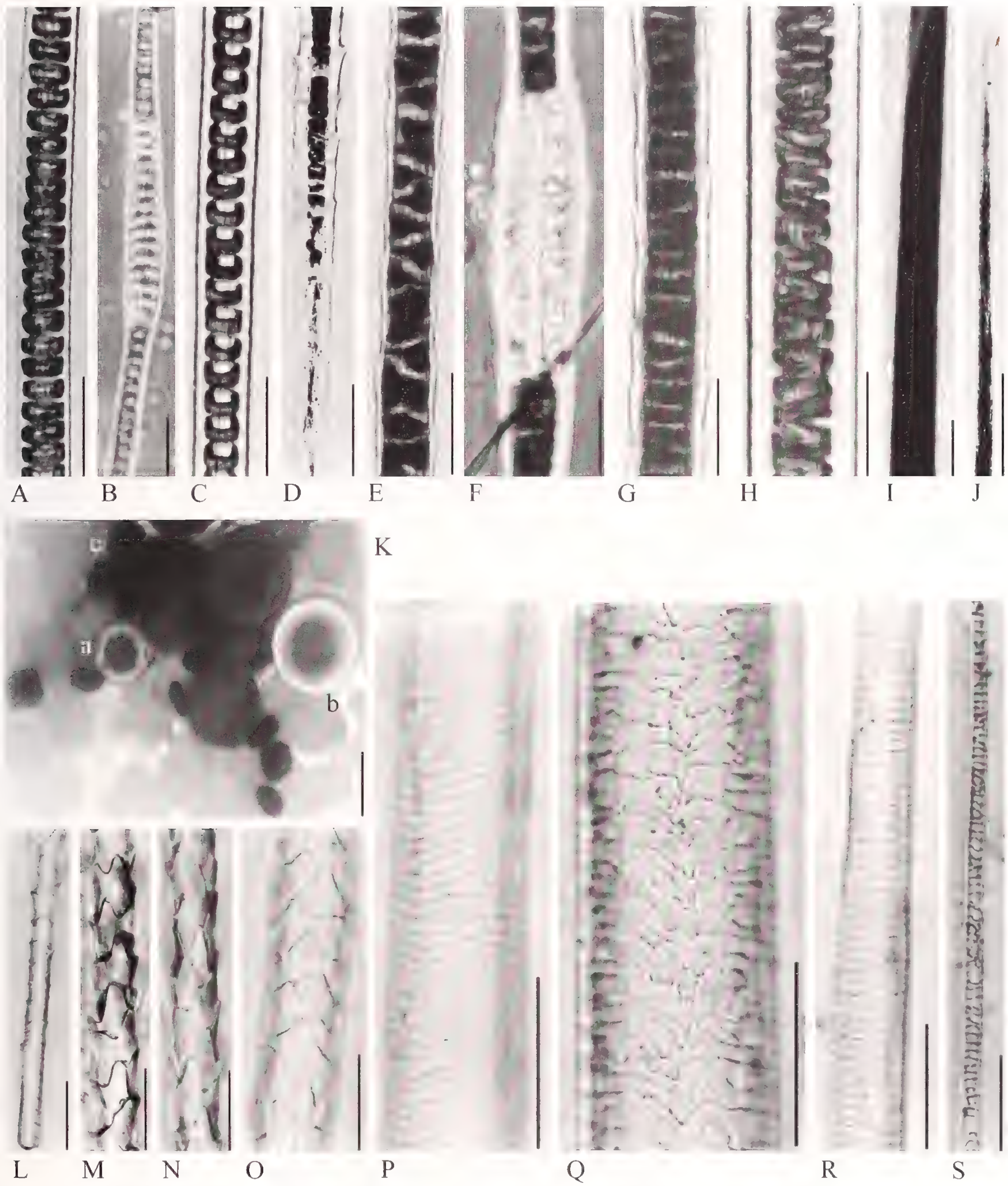
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Plate 7. Whole mounts, cross sections and cuticular scale casts of *Petrodromus tetradactylus* (bars equivalent to 50 µm).

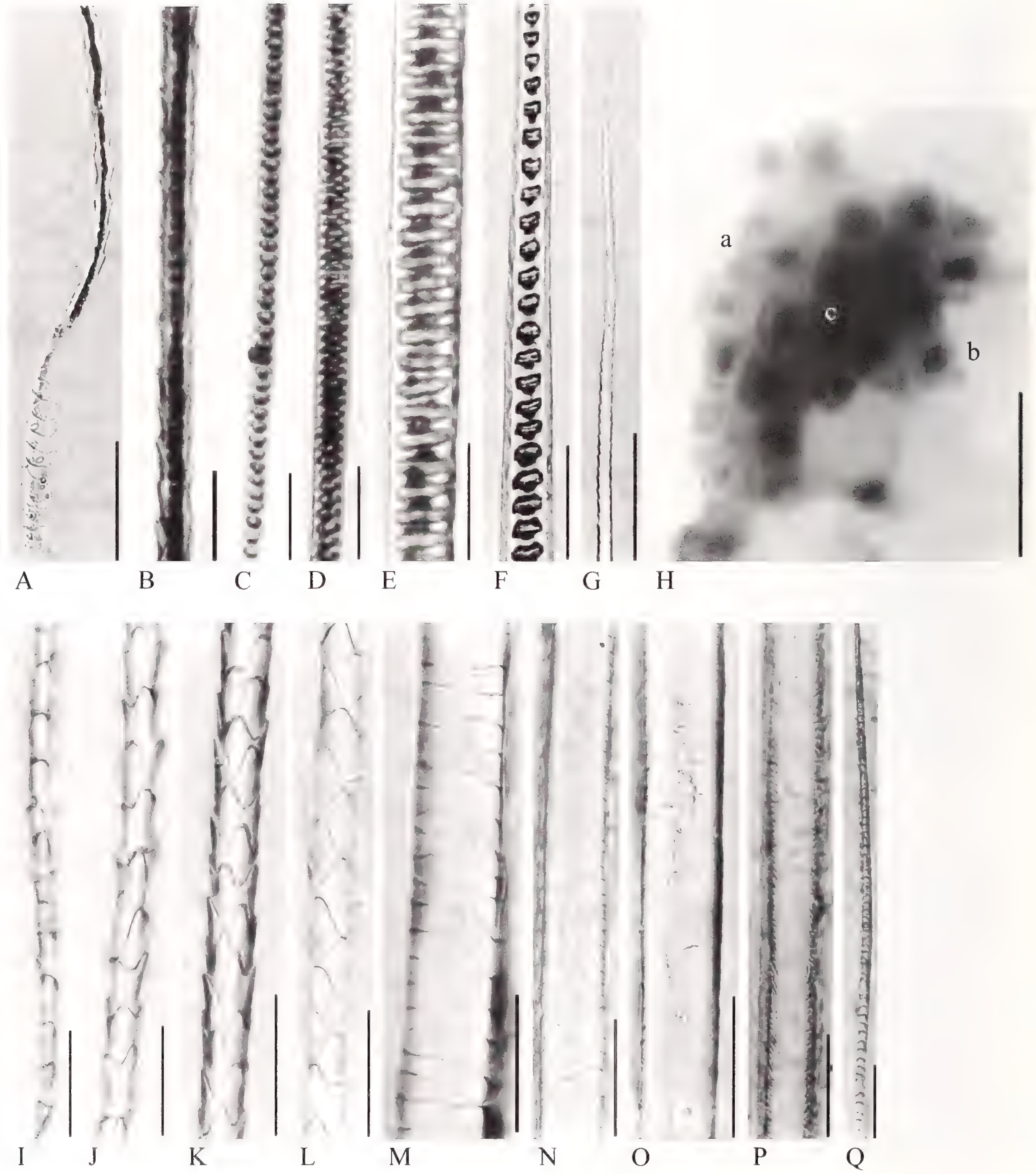
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Plate 8. Whole mounts, cross sections and cuticular scale casts of *Crocidura cyanea* (bars equivalent to 50 μm).

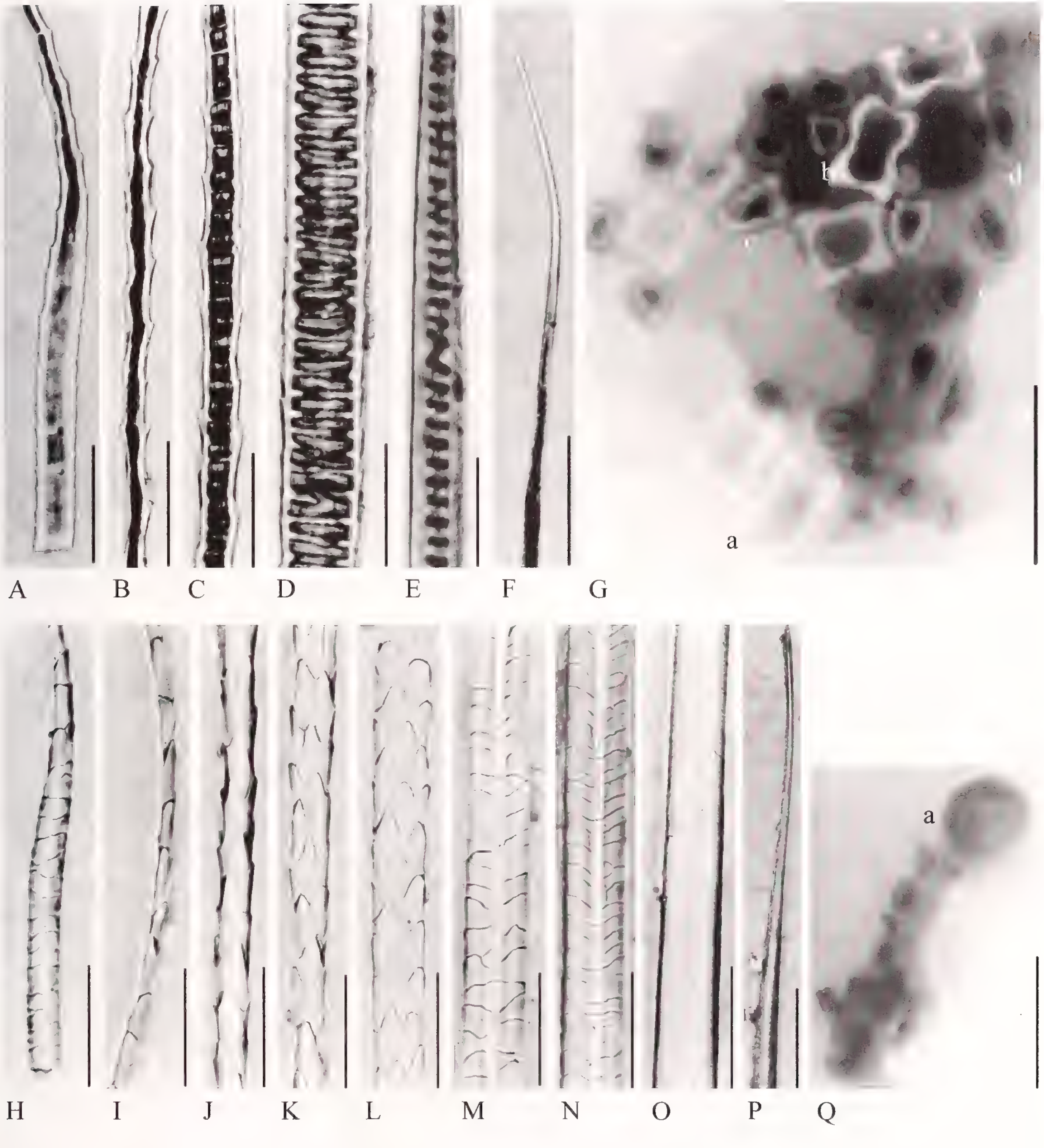
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Plate 9. Whole mounts, cross sections and cuticular scale casts of *Crocidura flavescens* (bars equivalent to 50 μm).

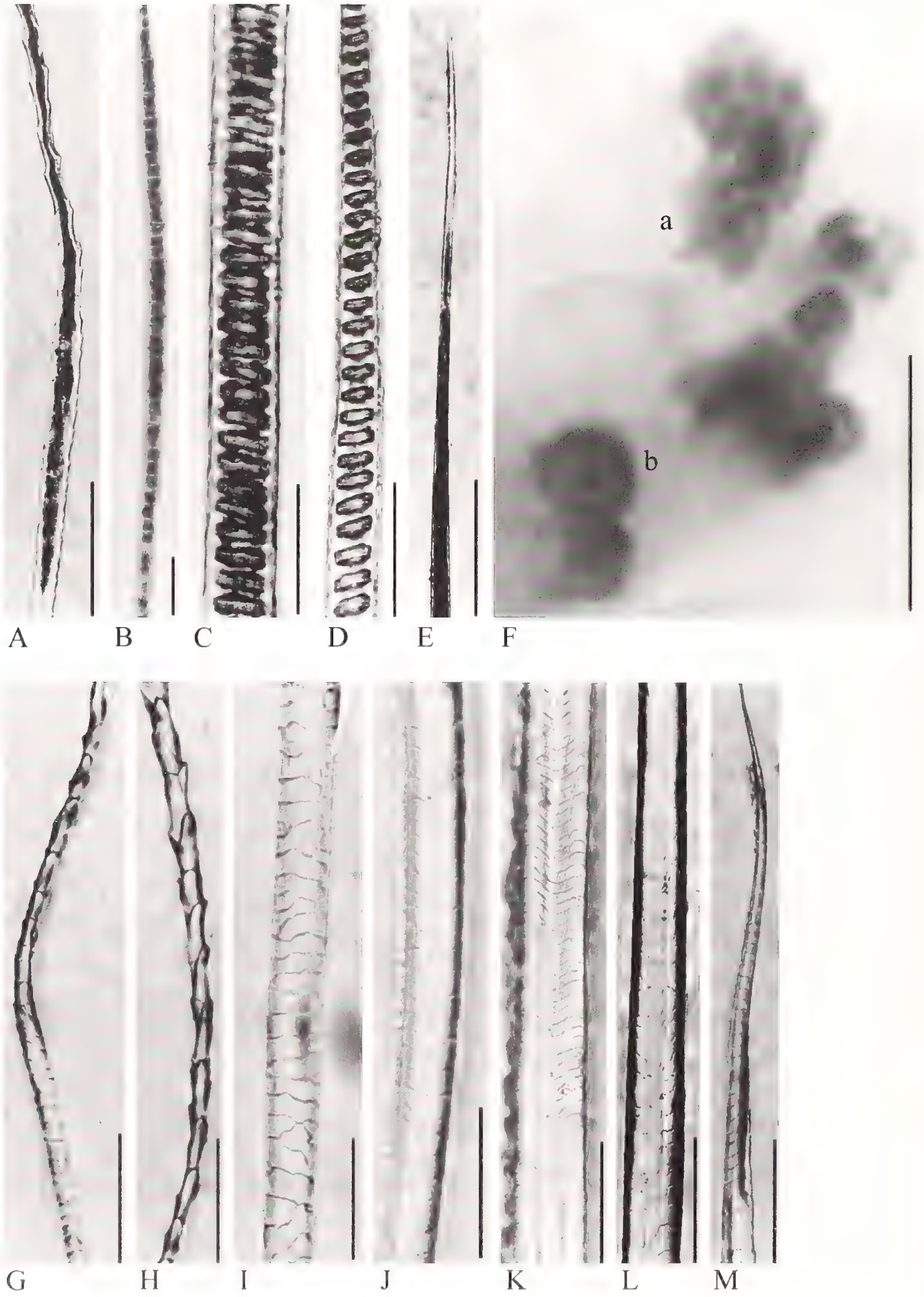
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Plate 10. Whole mounts, cross sections and cuticular scale casts of *Crocidura fuscomurina* (bars equivalent to 50 µm).

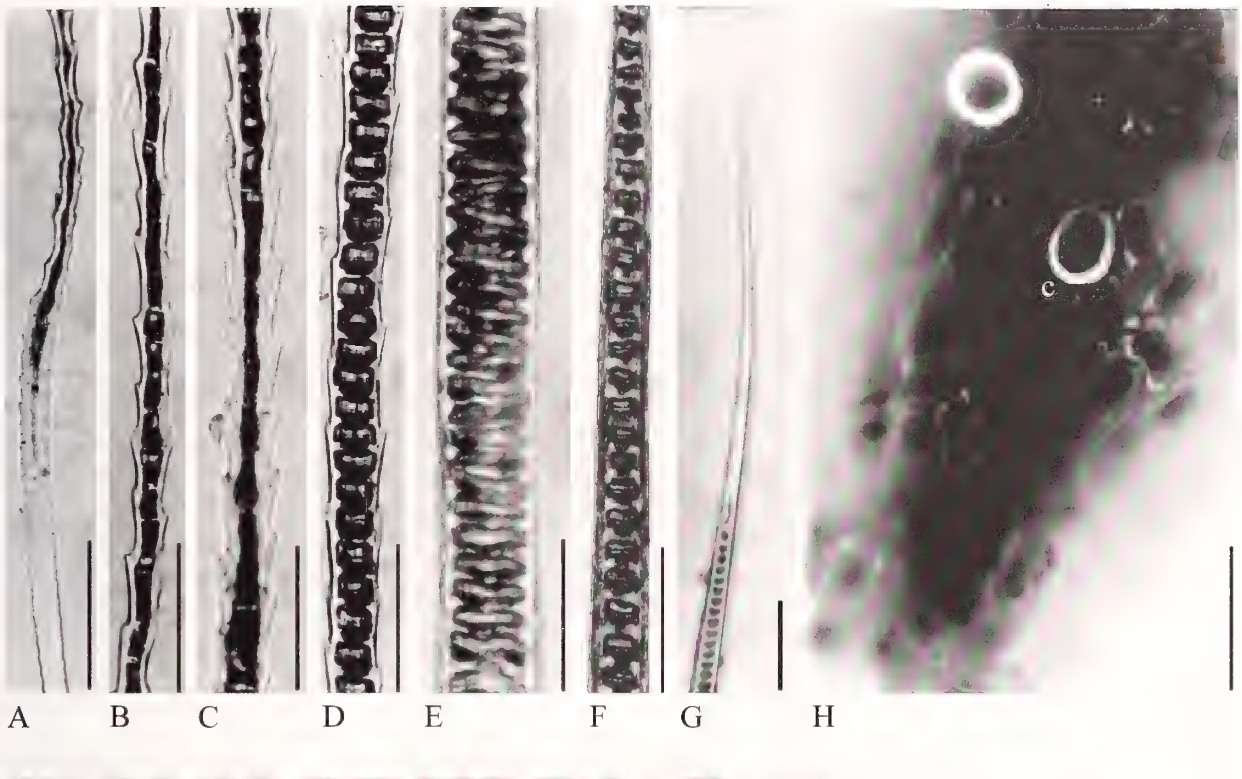
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Plate 11. Whole mounts, cross sections and cuticular scale casts of *Crocidura hirta* (bars equivalent to 50 µm).

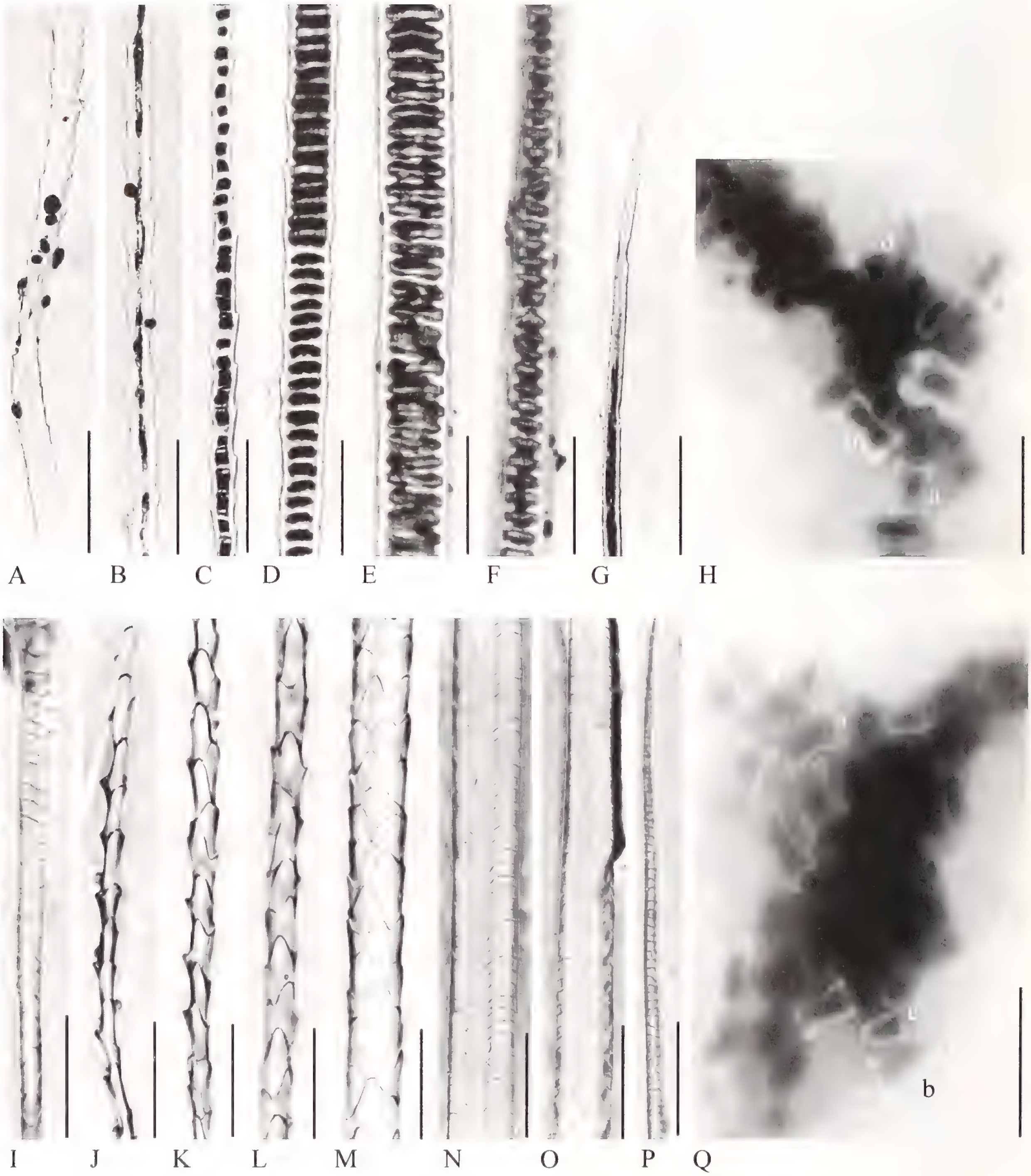
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Plate 12. Whole mounts, cross sections and cuticular scale casts of *Crocidura luna* (bars equivalent to 50 µm).

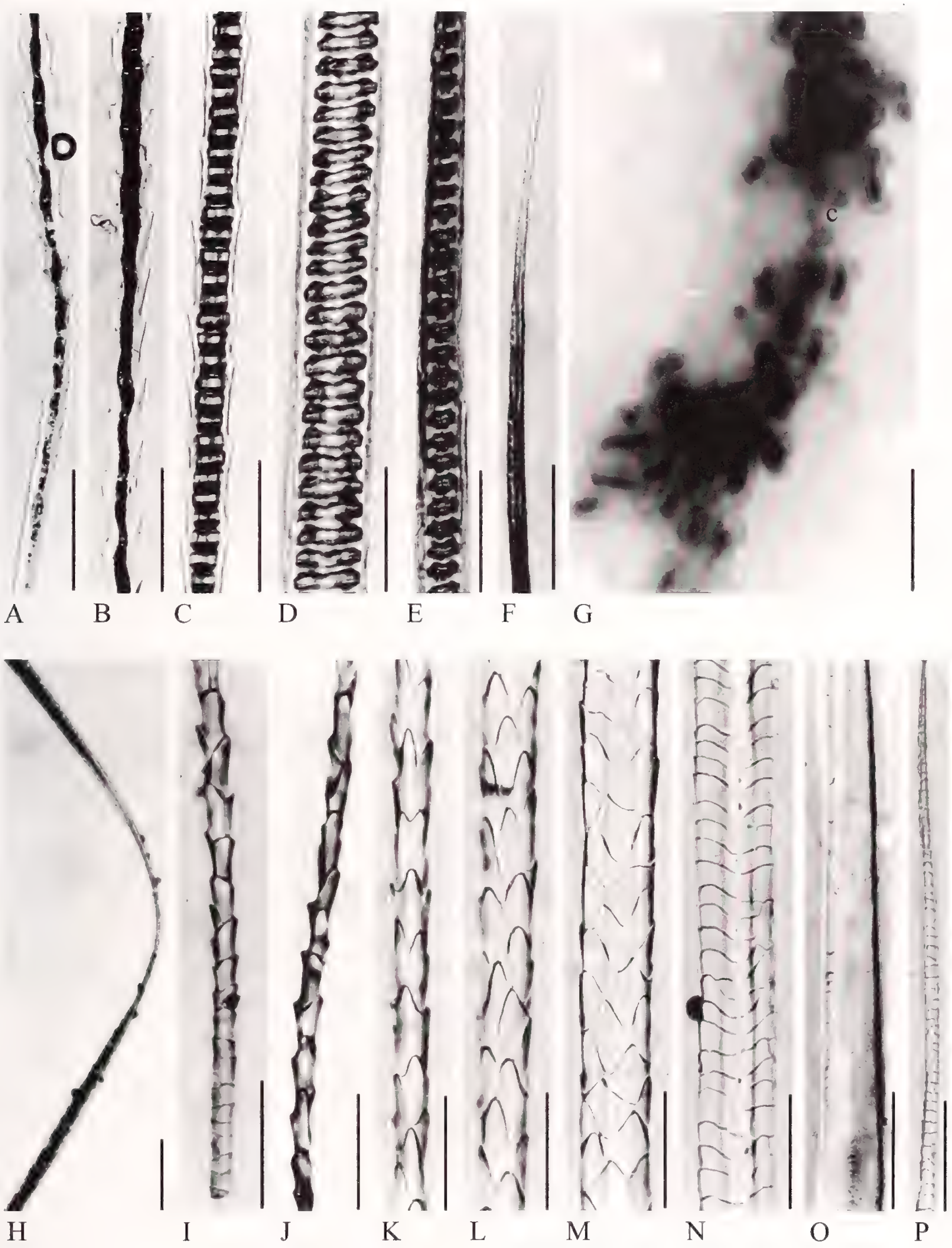

Plate 13. Whole mounts, cross sections and cuticular scale casts of *Crocidura maquassiensis* (bars equivalent to 50 µm).

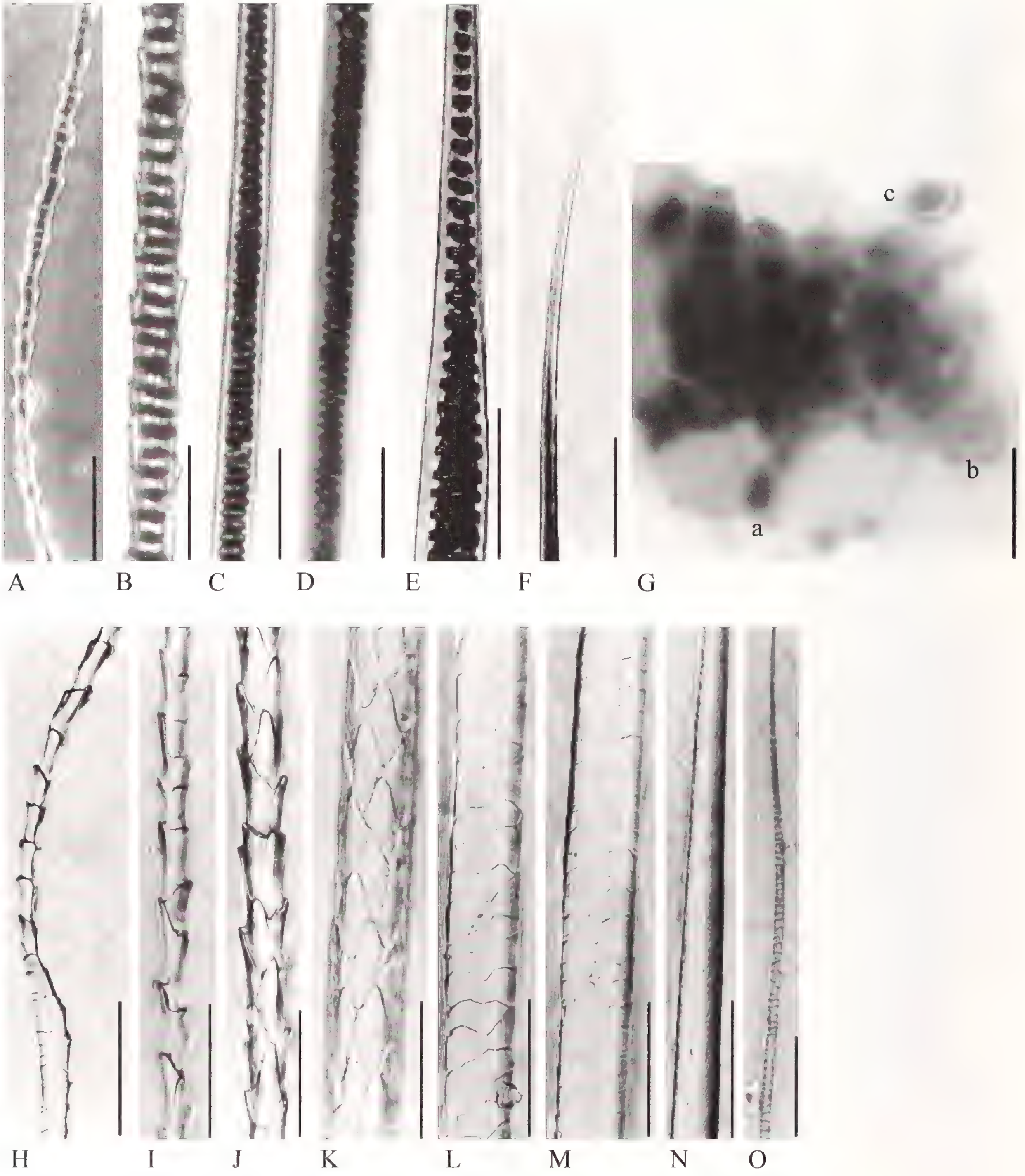
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Plate 14. Whole mounts, cross sections and cuticular scale casts of *Crocidura mariquensis* (bars equivalent to 50 µm).

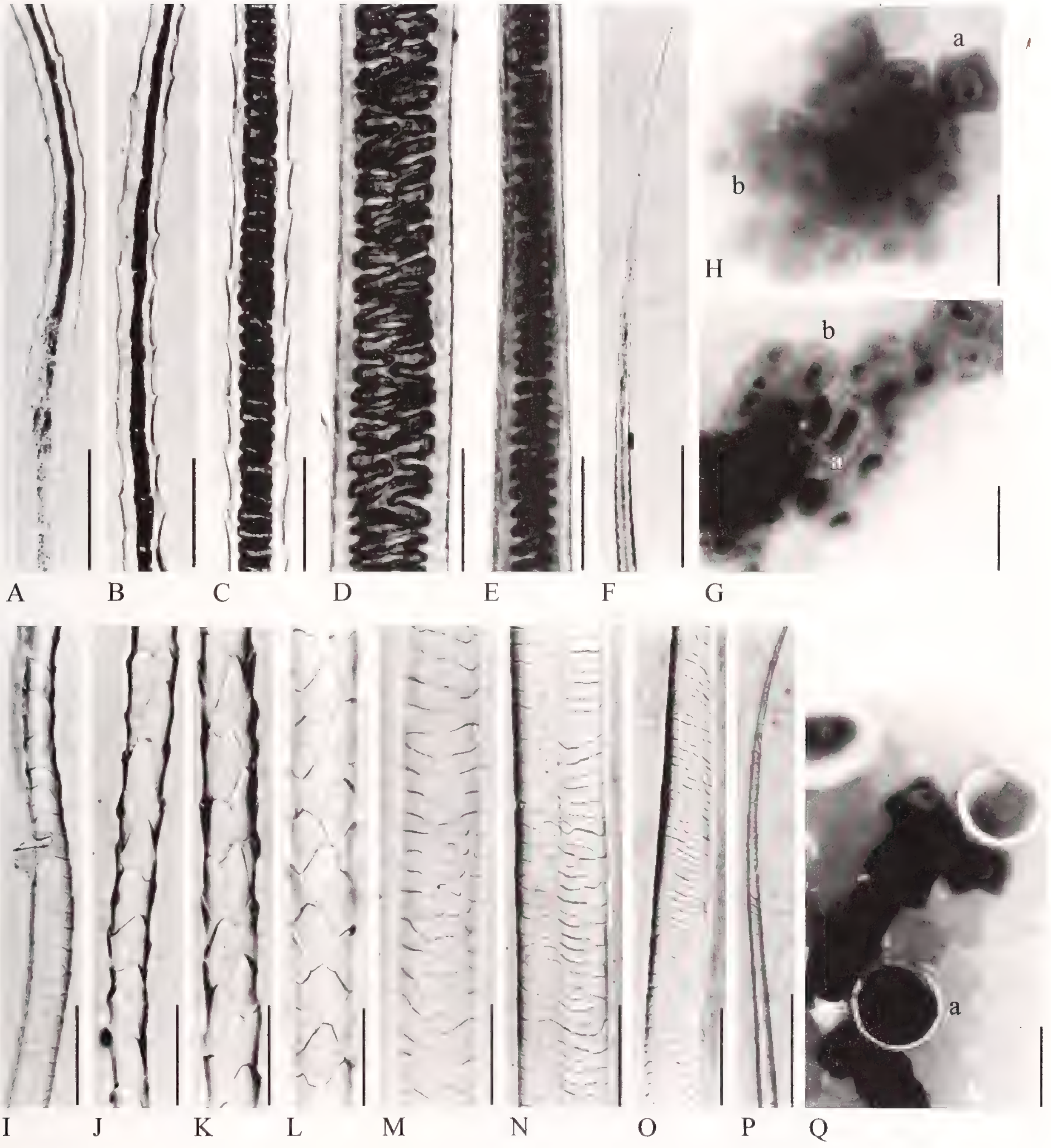
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Plate 15. Whole mounts, cross sections and cuticular scale casts of *Crocidura olivieri martiensseni* (bars equivalent to 50 µm).

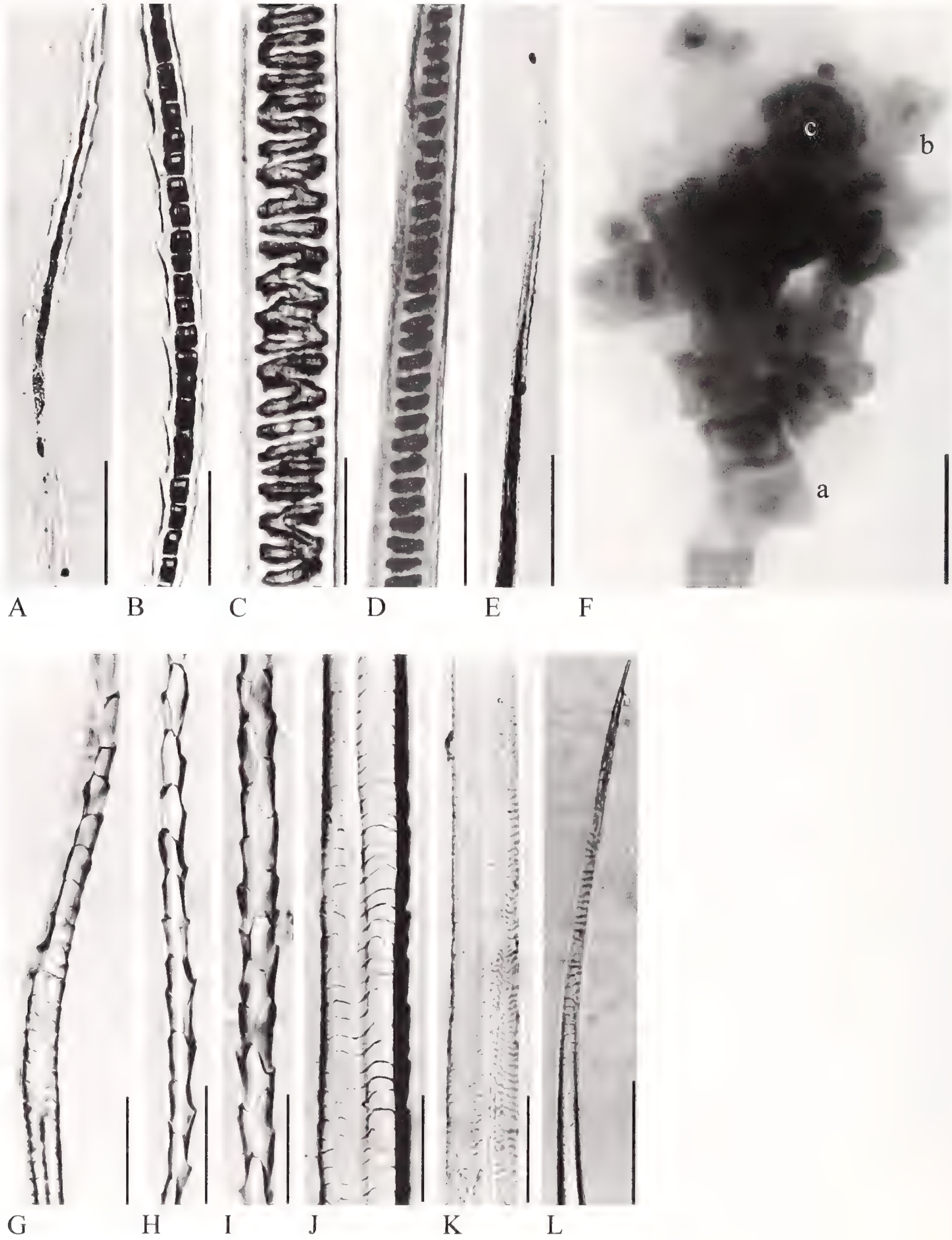

Plate 16. Whole mounts, cross sections and cuticular scale casts of *Crocidura olivieri occidentalis* (bars equivalent to 50 µm).

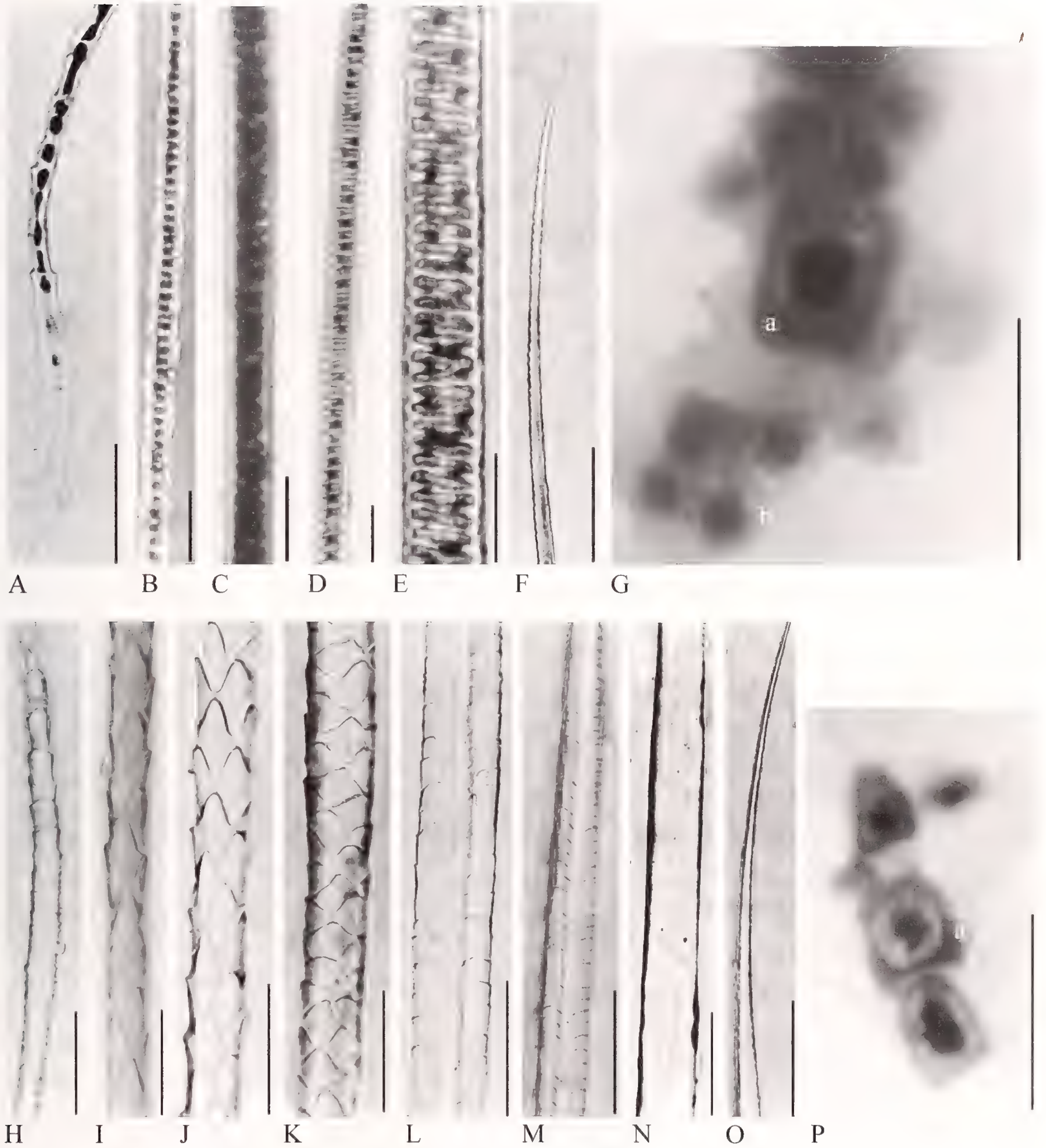
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Plate 17. Whole mounts, cross sections and cuticular scale casts of *Crocidura silacea* (bars equivalent to 50 µm).

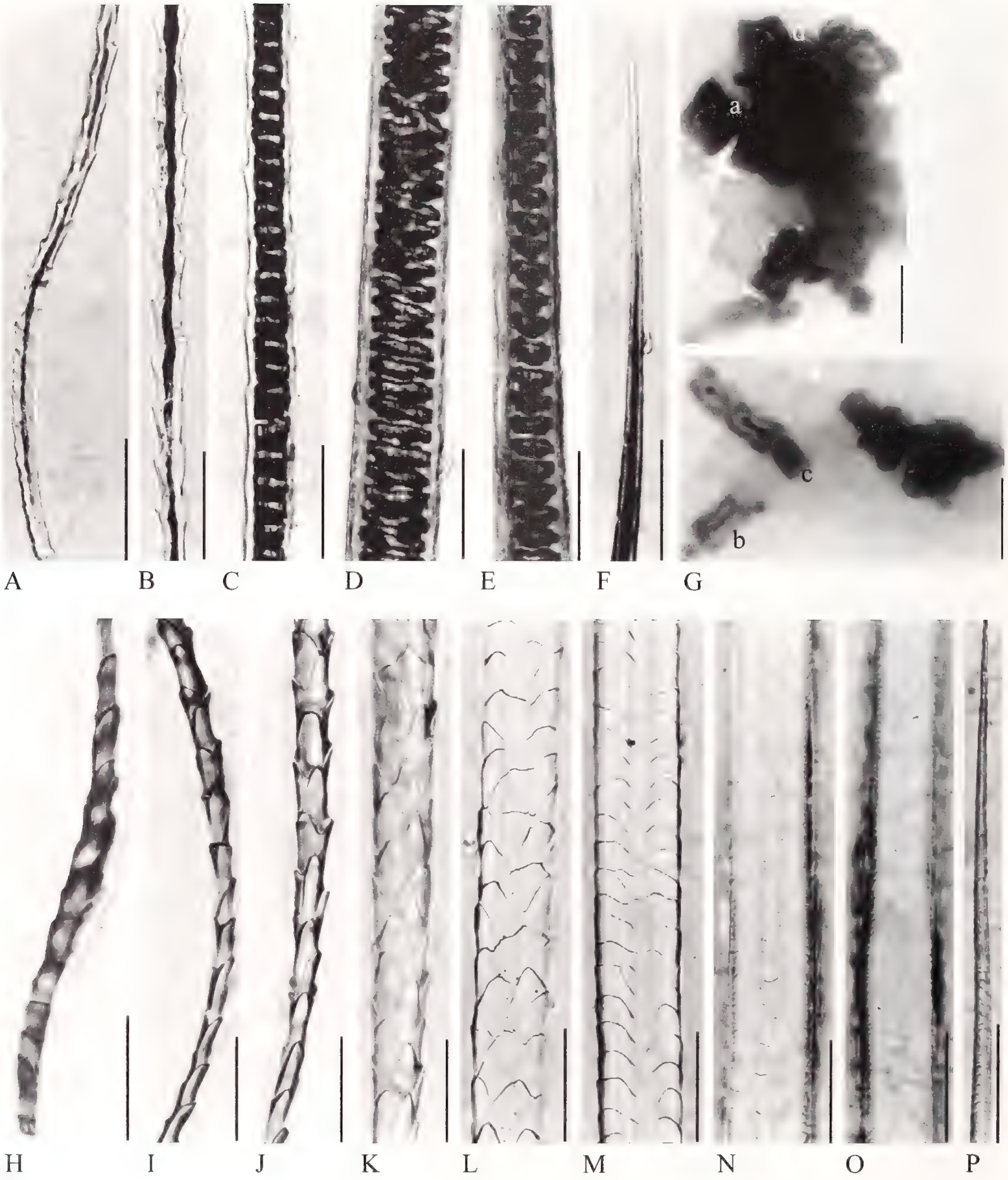
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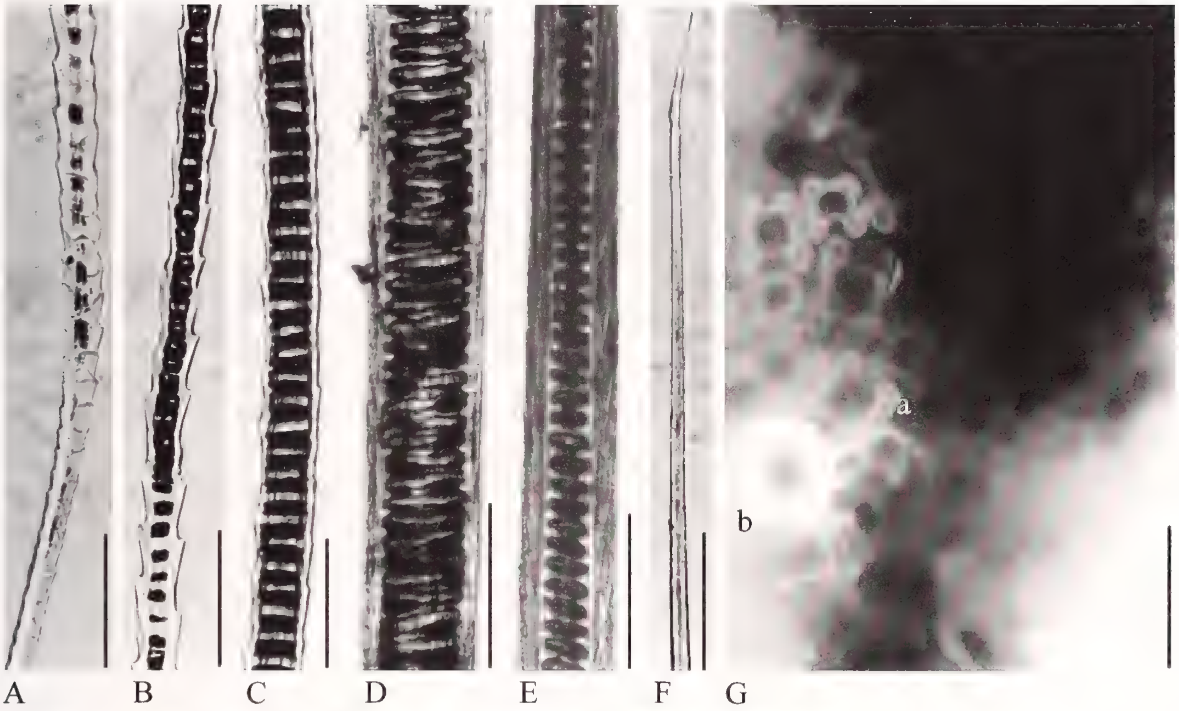
Plate 18. Whole mounts, cross sections and cuticular scale casts of *Crocidura turba* (bars equivalent to 50 µm).



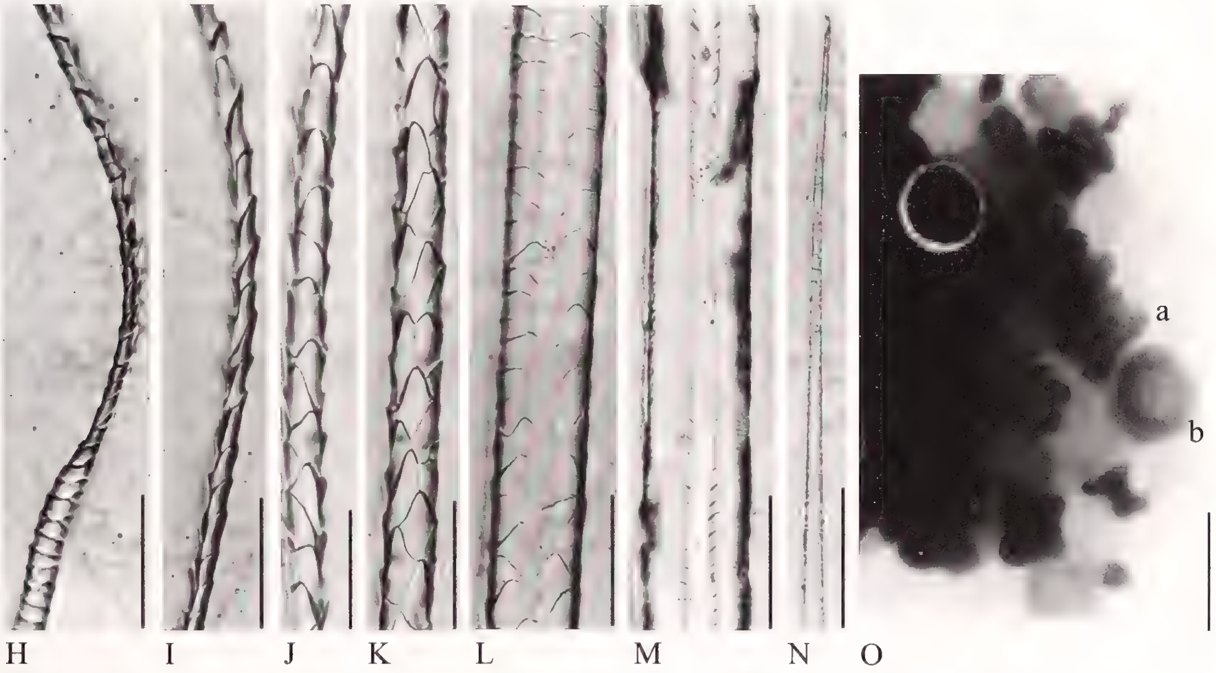

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Plate 19. Whole mounts, cross sections and cuticular scale casts of *Myosorex cafer* (bars equivalent to 50 μm).

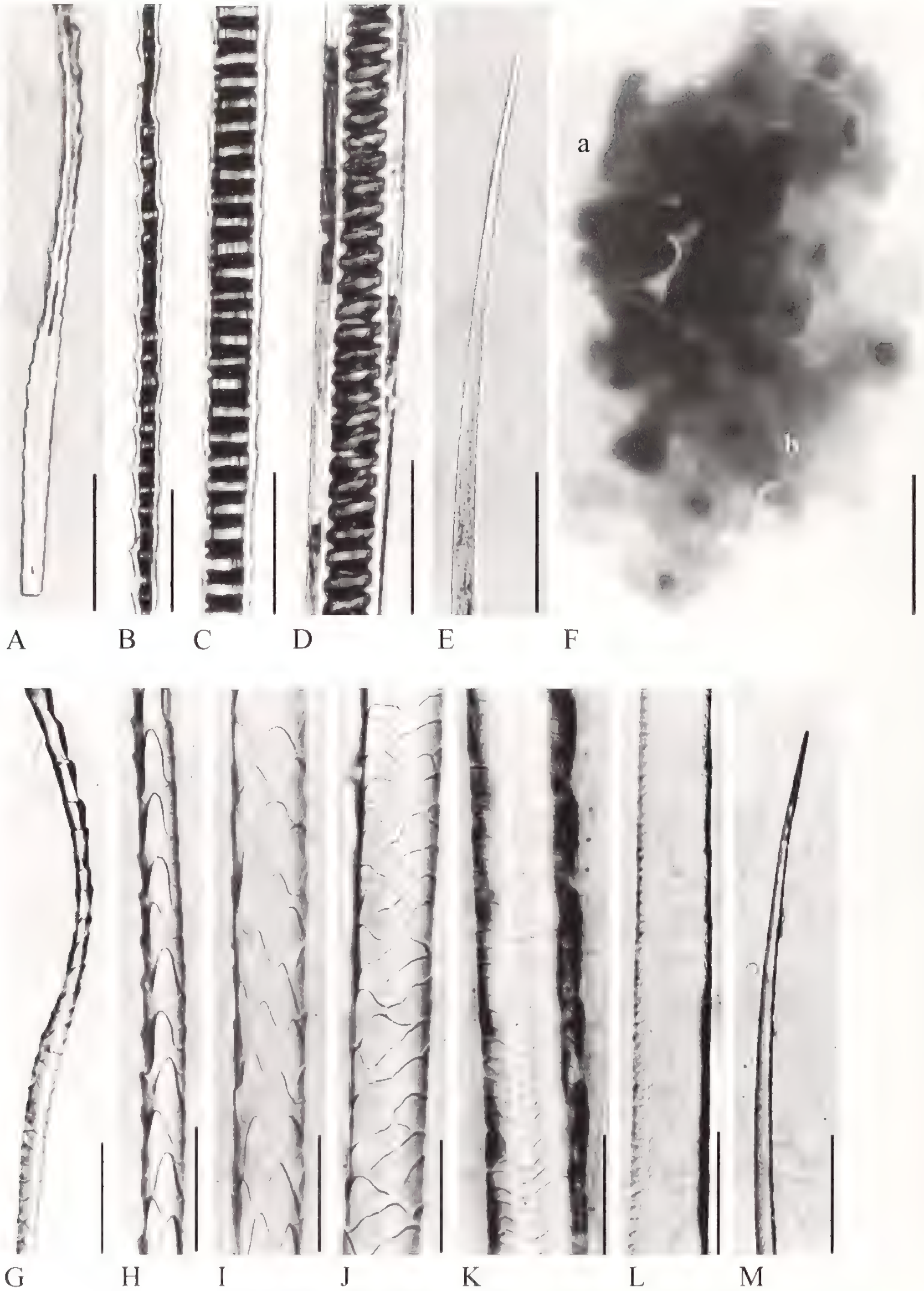
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Plate 20. Whole mounts, cross sections and cuticular scale casts of *Myosorex longicaudatus* (bars equivalent to 50 µm).

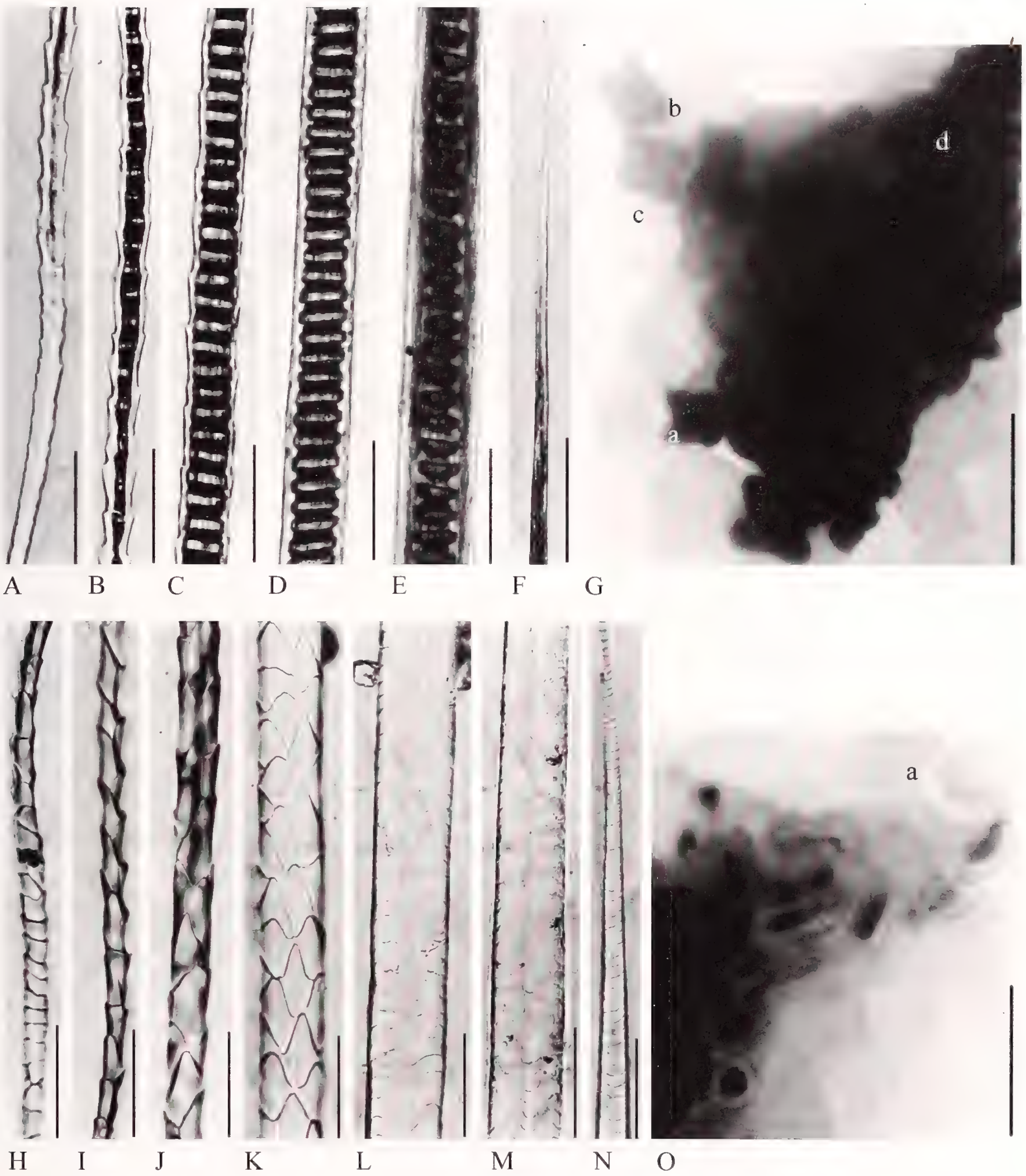
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Plate 21. Whole mounts, cross sections and cuticular scale casts of *Myosorex sclateri* (bars equivalent to 50 µm).

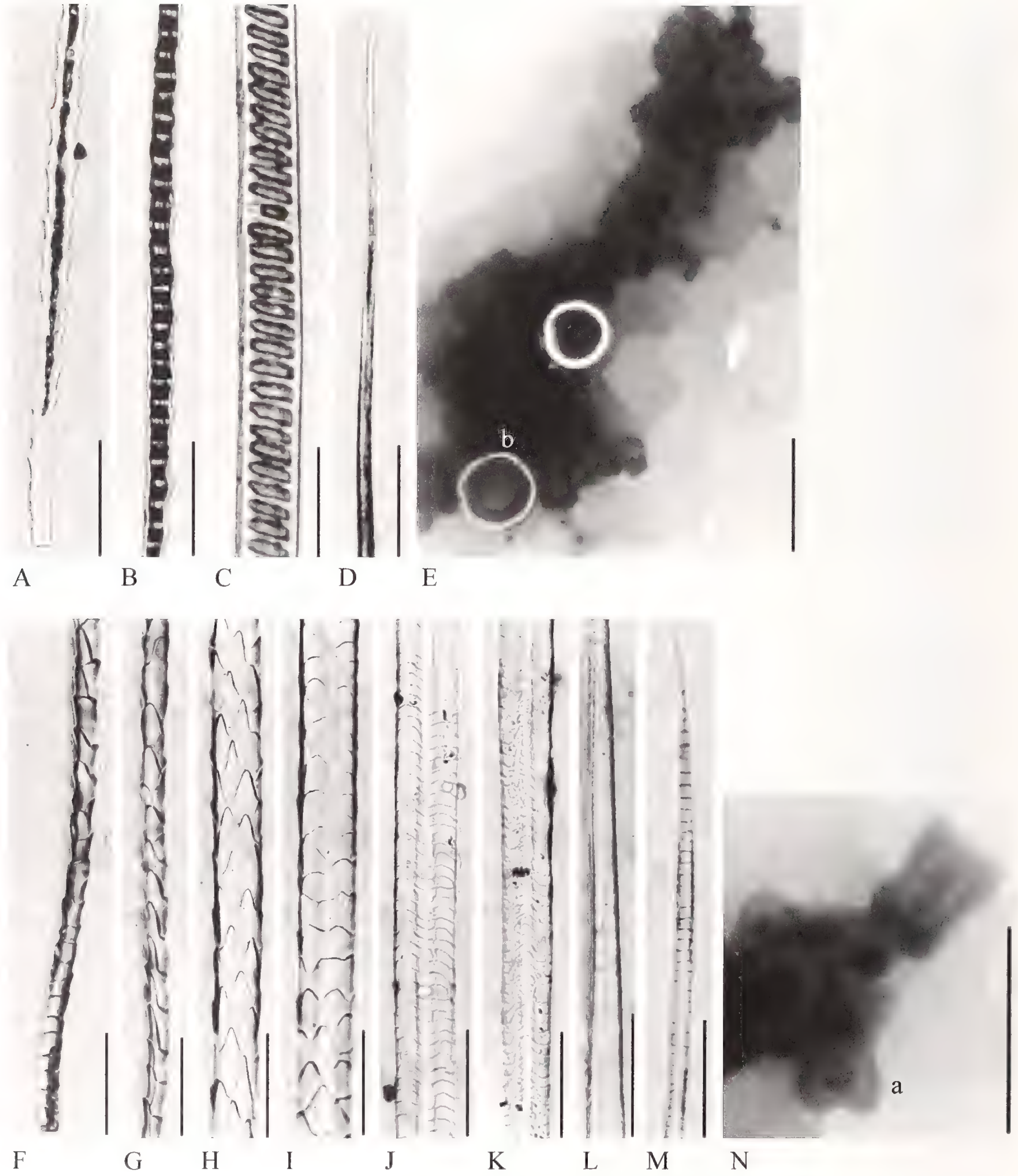
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Plate 22. Whole mounts, cross sections and cuticular scale casts of *Myosorex tenuis* (bars equivalent to 50 µm).

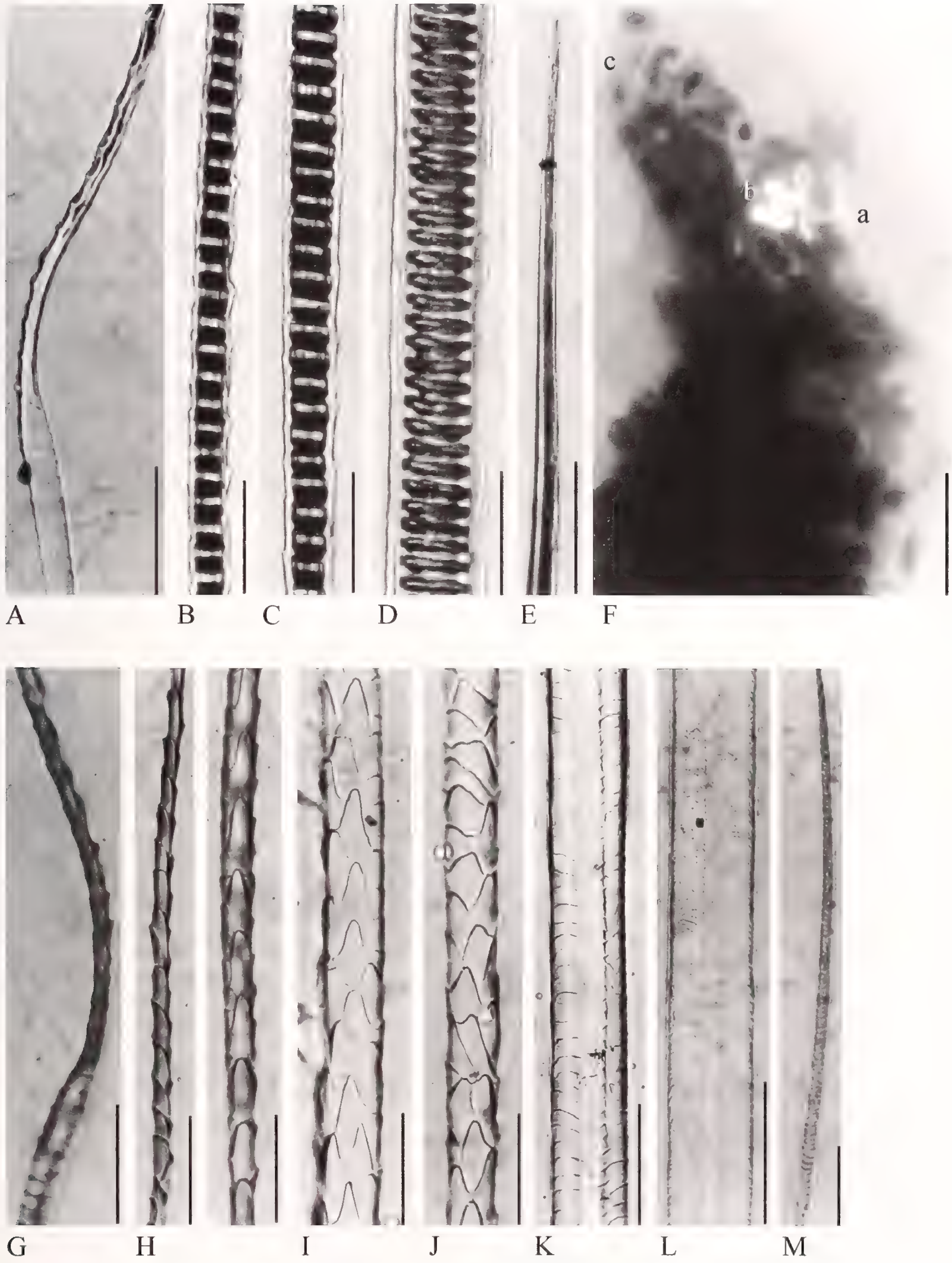

Plate 23. Whole mounts, cross sections and cuticular scale casts of *Myosorex varius* (bars equivalent to 50 µm).

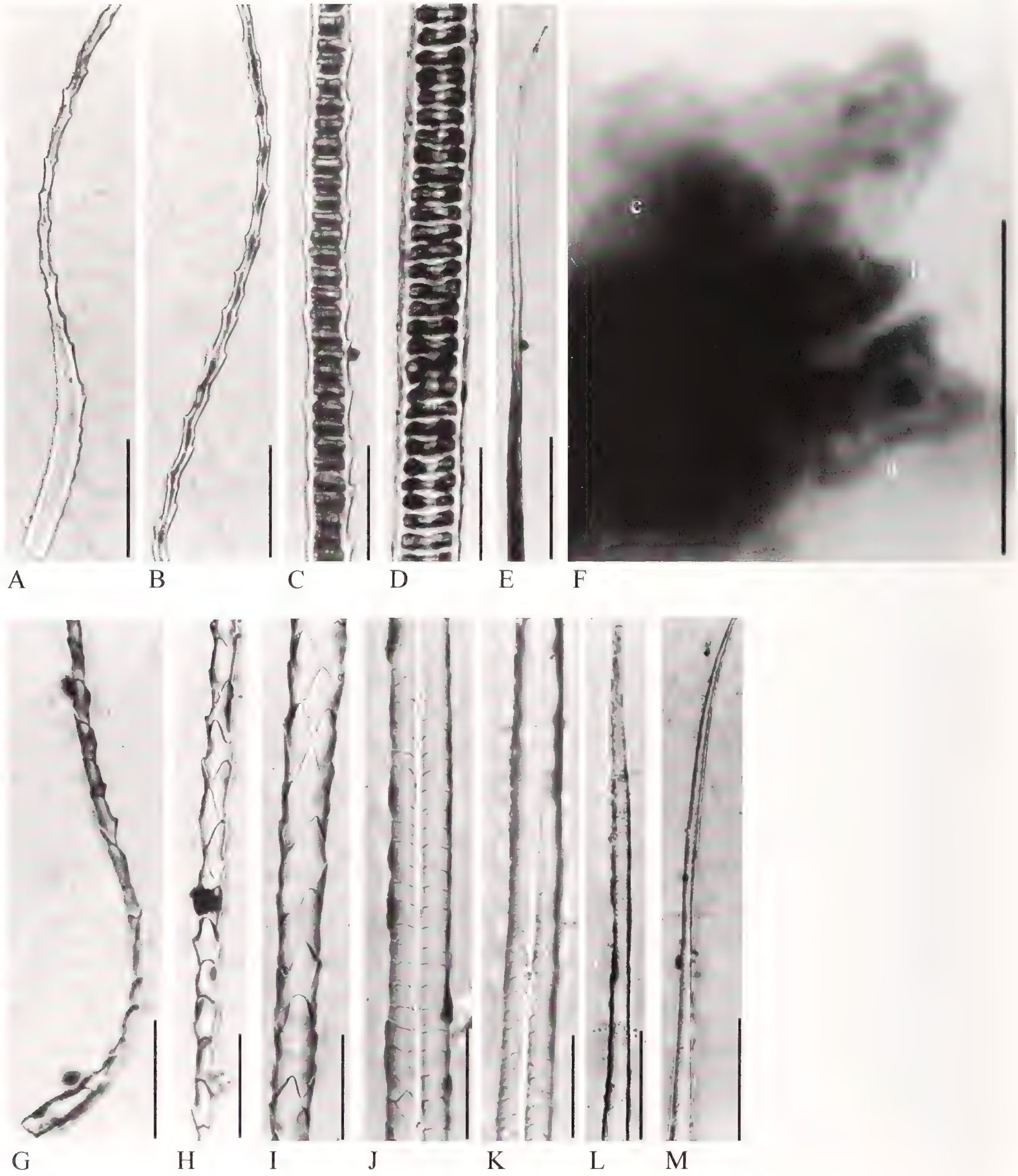

Plate 24. Whole mounts, cross sections and cuticular scale casts of *Suncus infinitesimus* (bars equivalent to 50 µm).

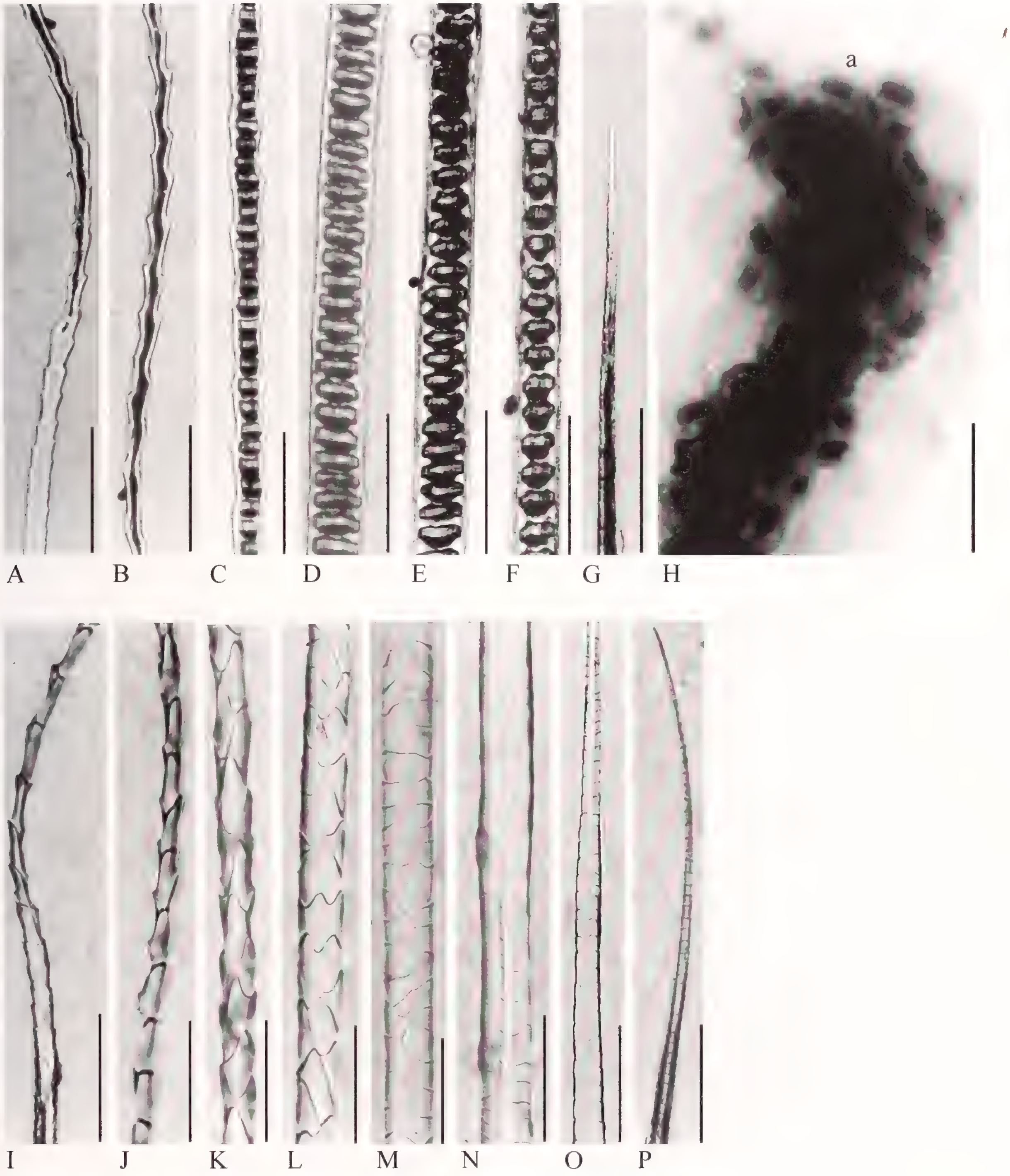
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Plate 25. Whole mounts, cross sections and cuticular scale casts of *Suncus lixus* (bars equivalent to 50 µm).

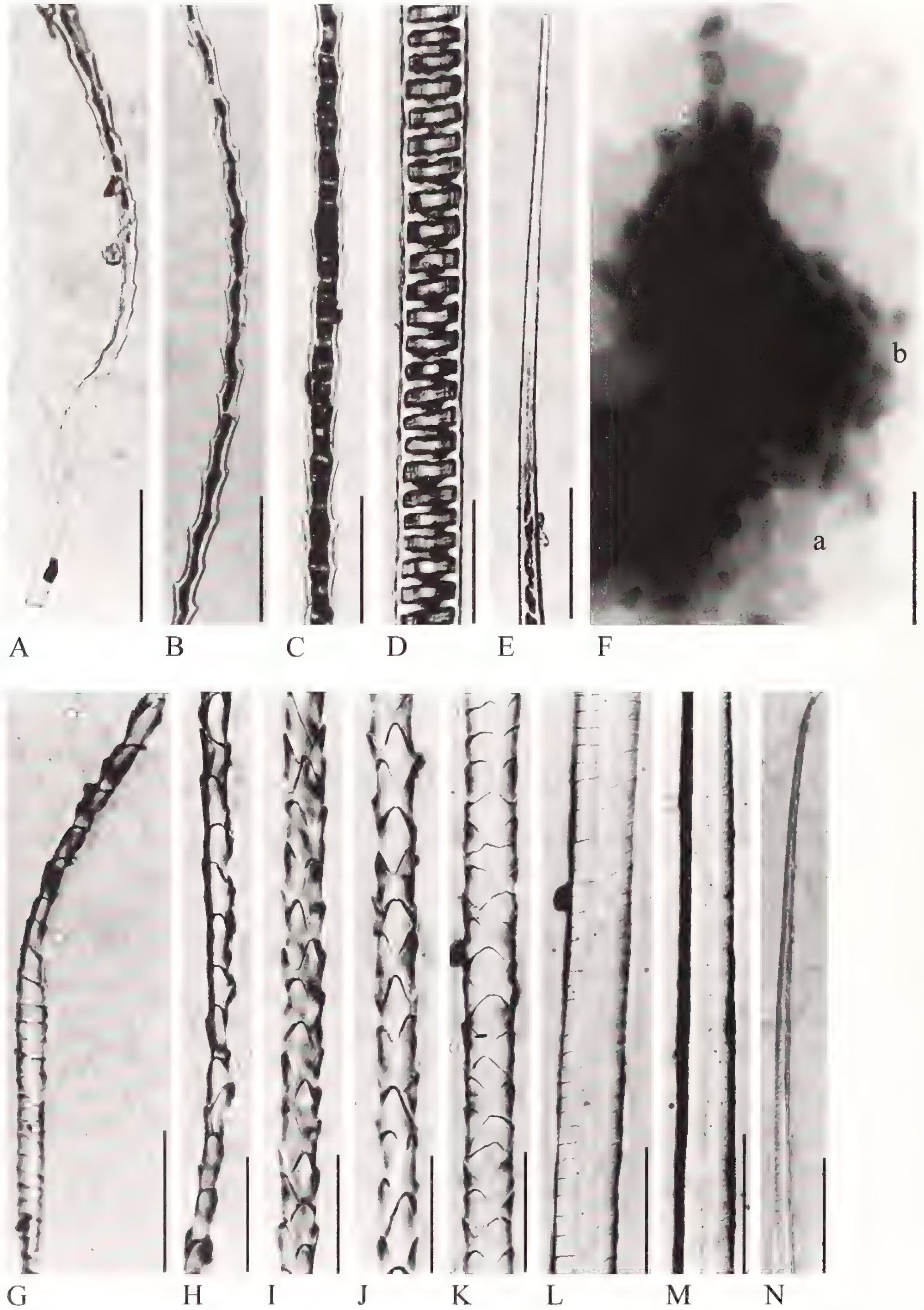
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Plate 26. Whole mounts, cross sections and cuticular scale casts of *Suncus varilla* (bars equivalent to 50 µm).

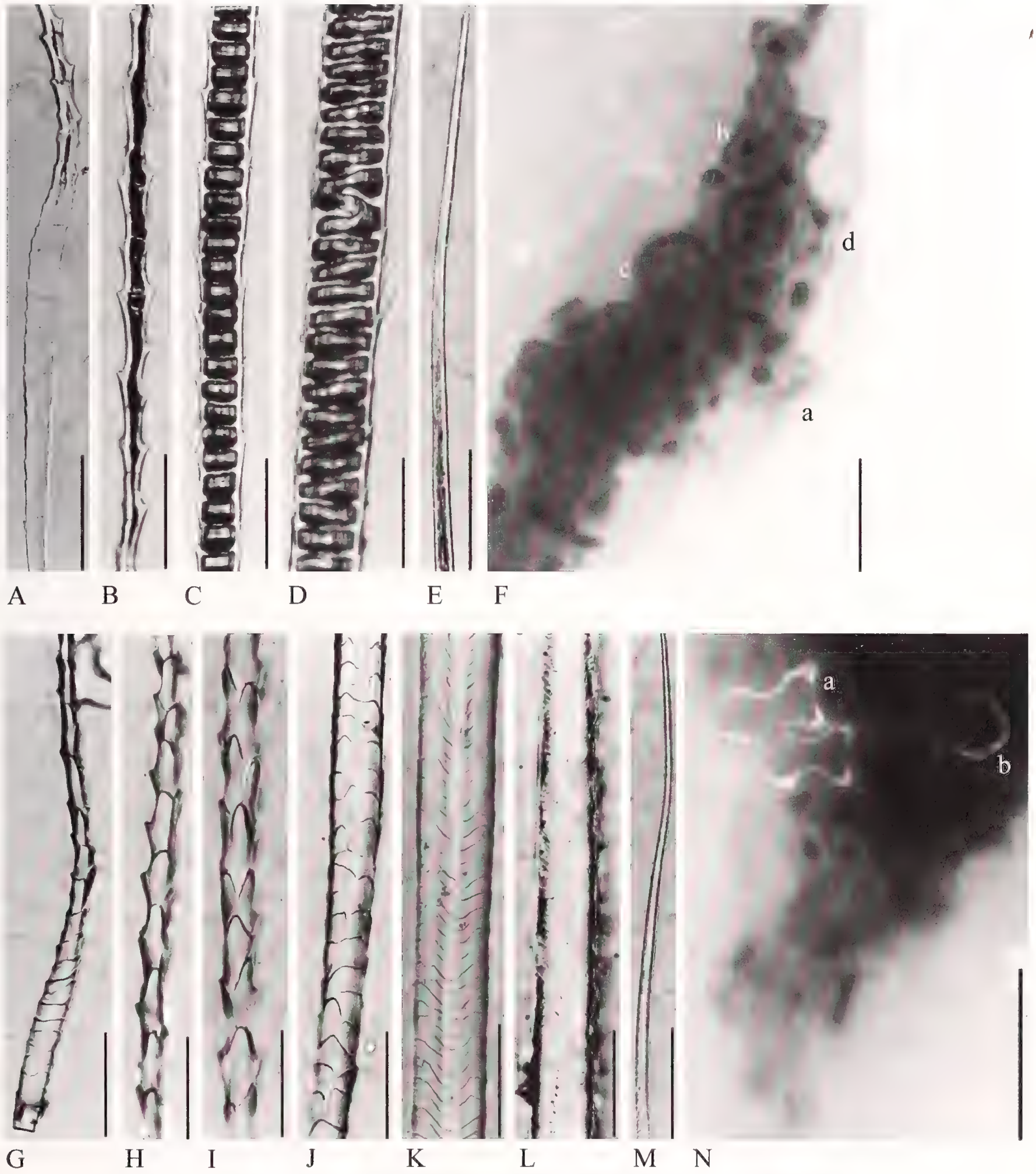
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Plate 27. Whole mounts, cross sections and cuticular scale casts of *Sylvisorex megalura* (bars equivalent to 50 µm).

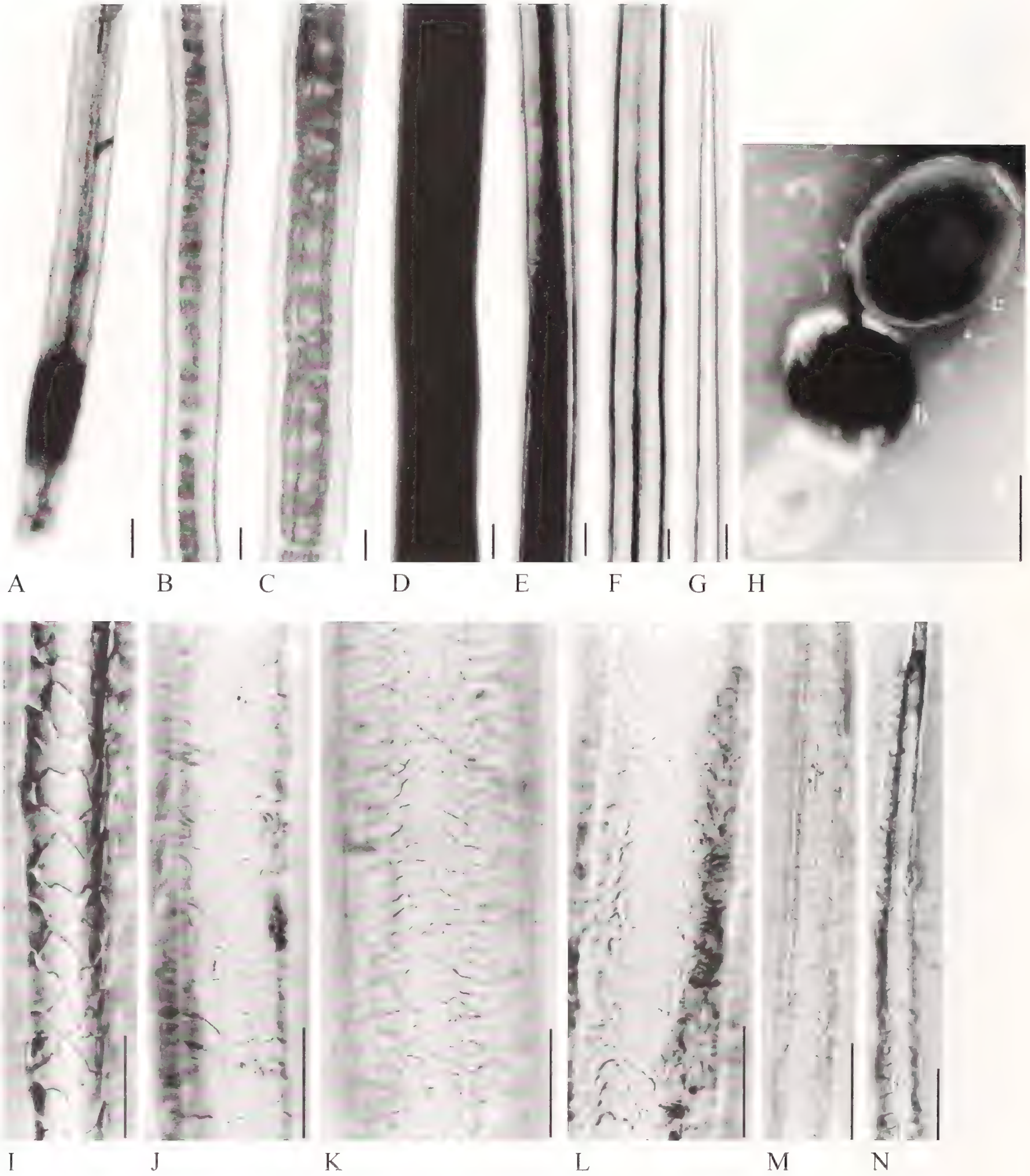
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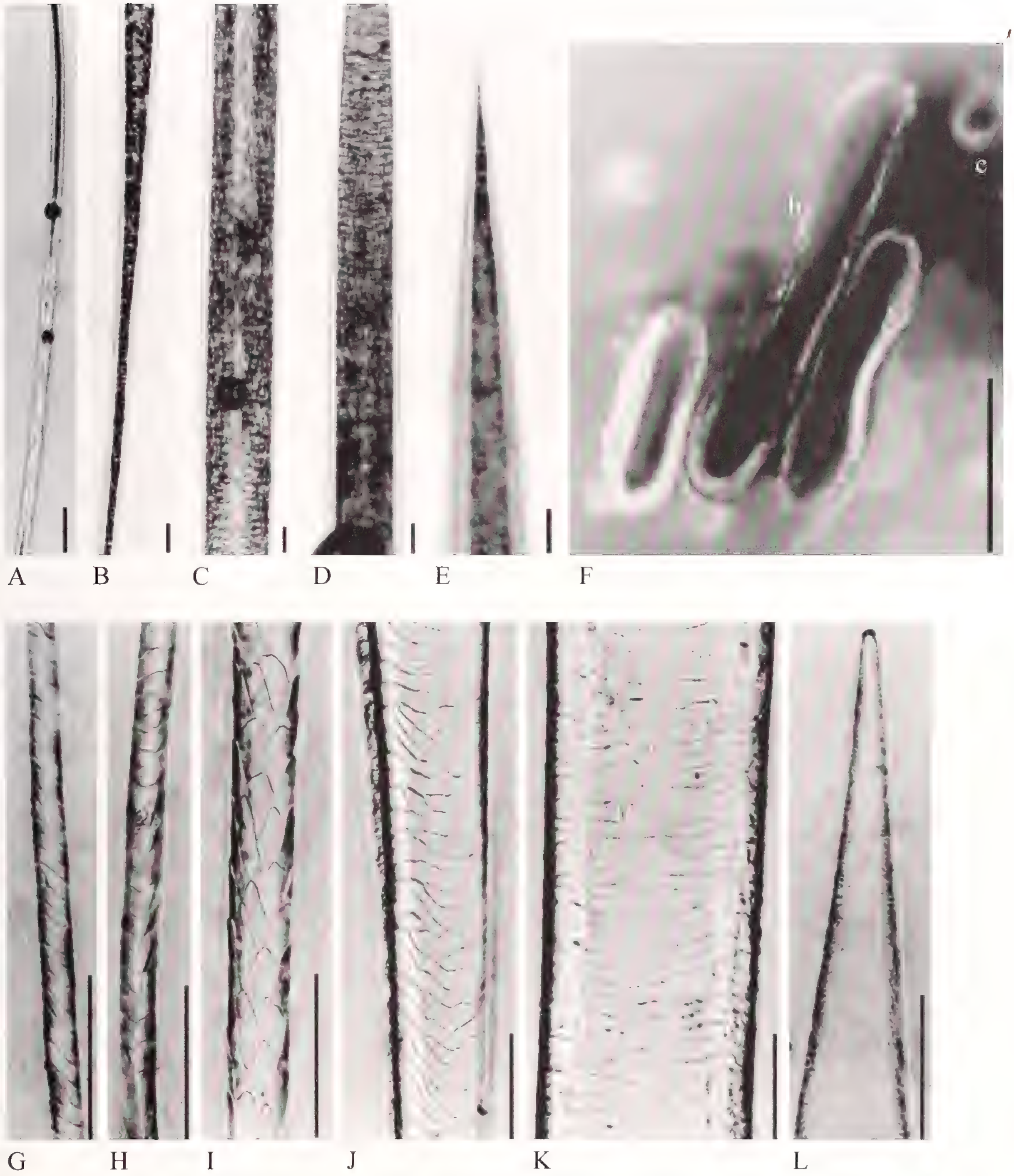
Plate 28. Whole mounts, cross sections and cuticular scale casts of *Atelerix frontalis* (bars equivalent to 50 μm).



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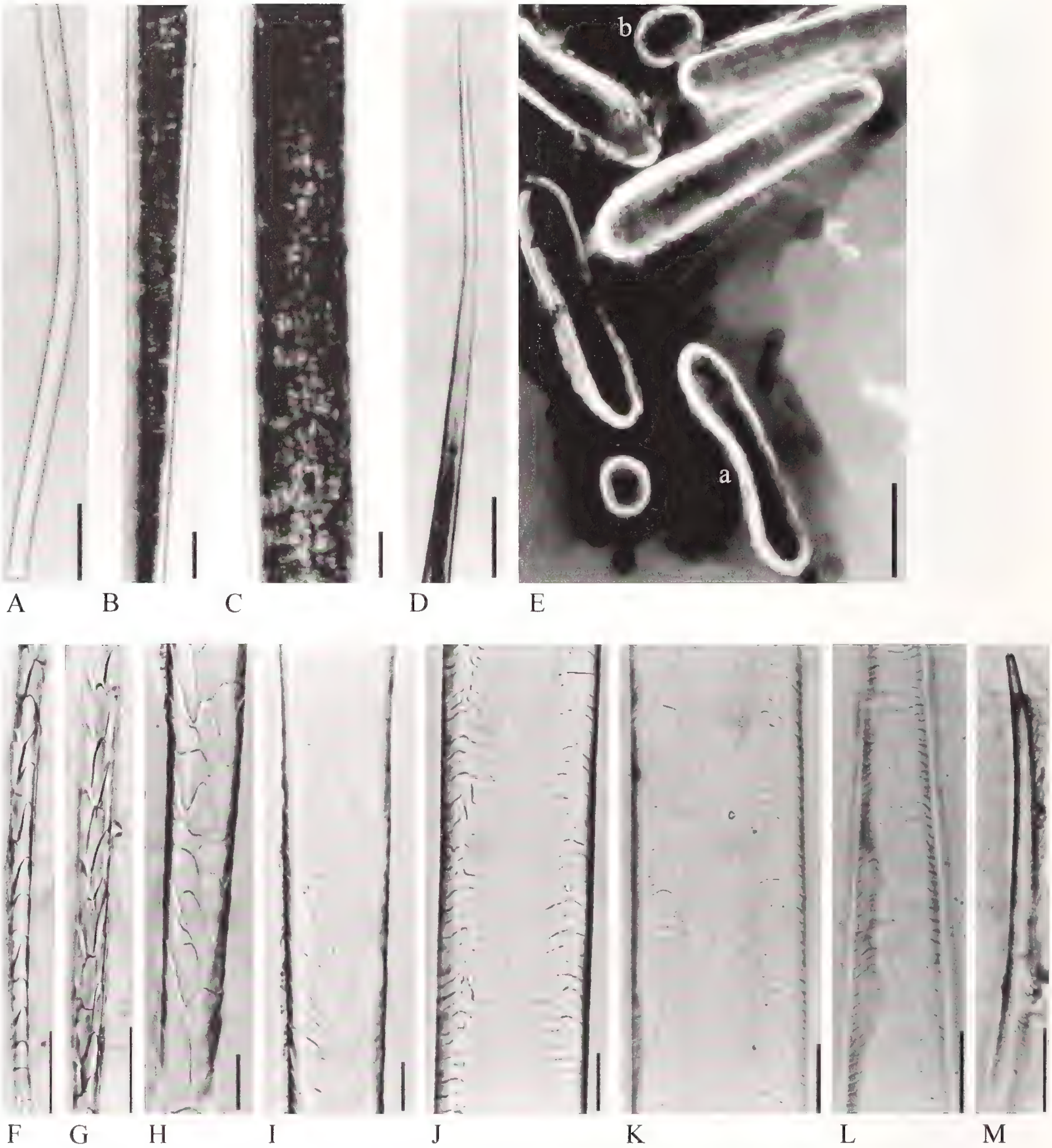
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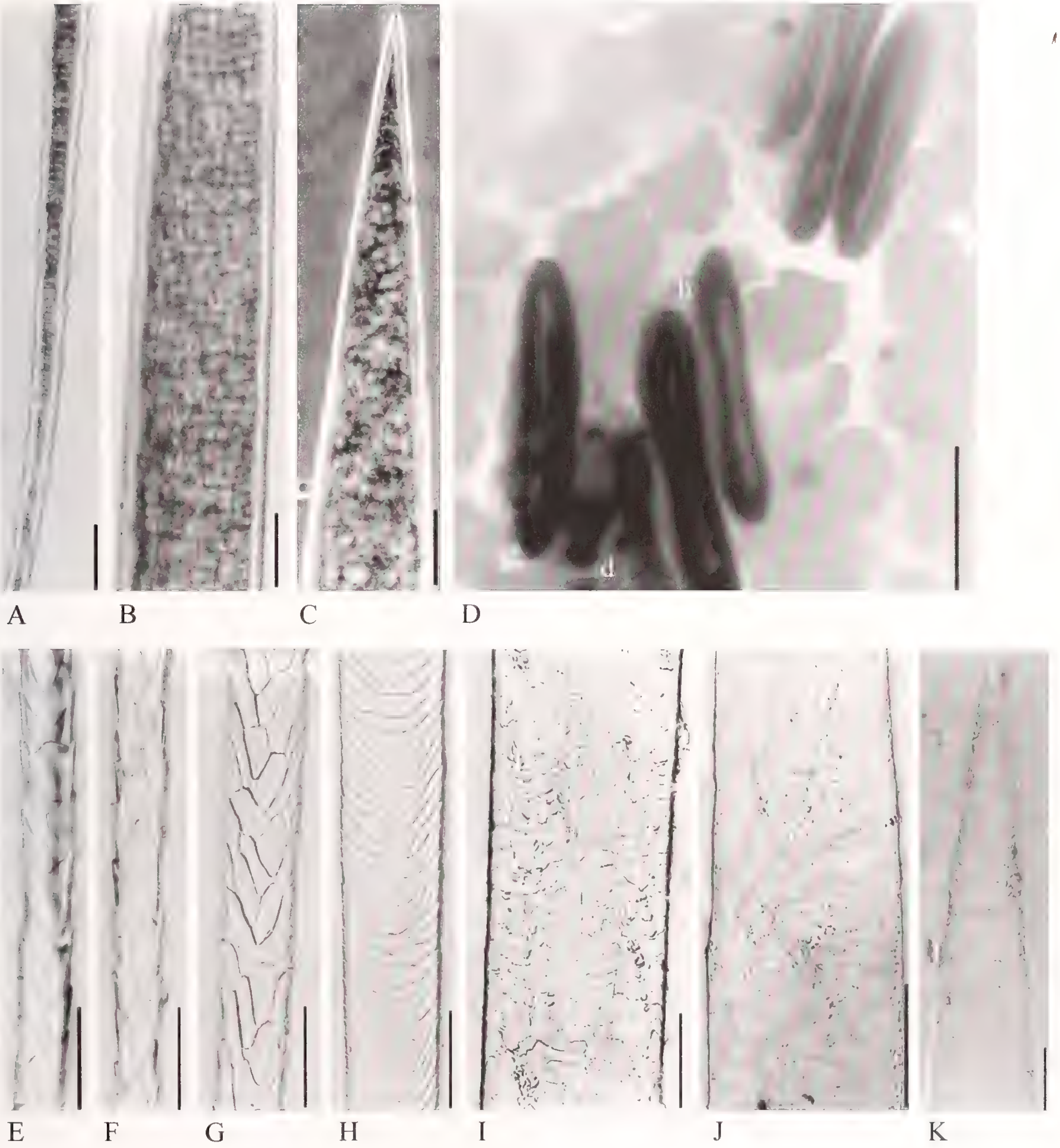

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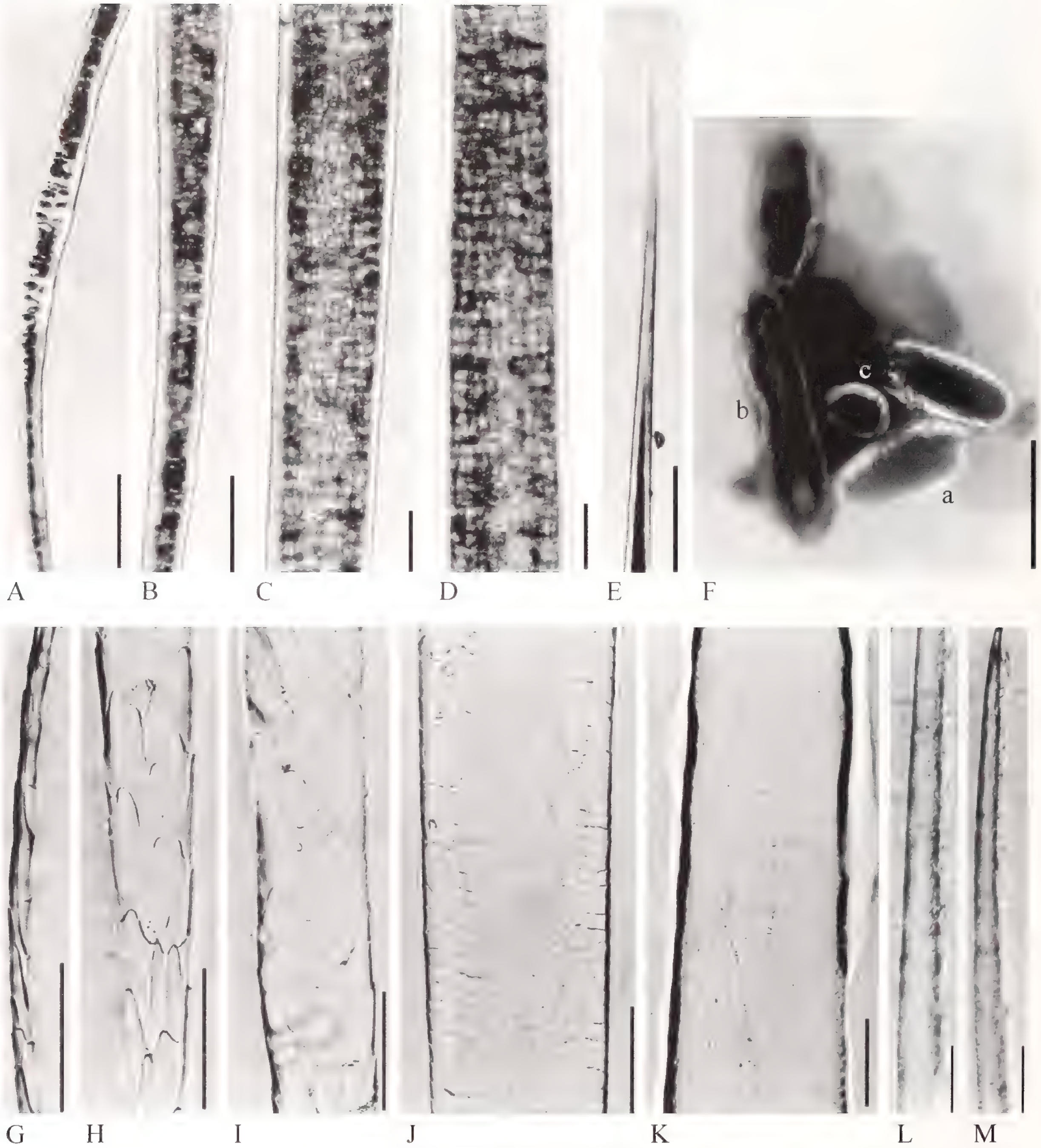
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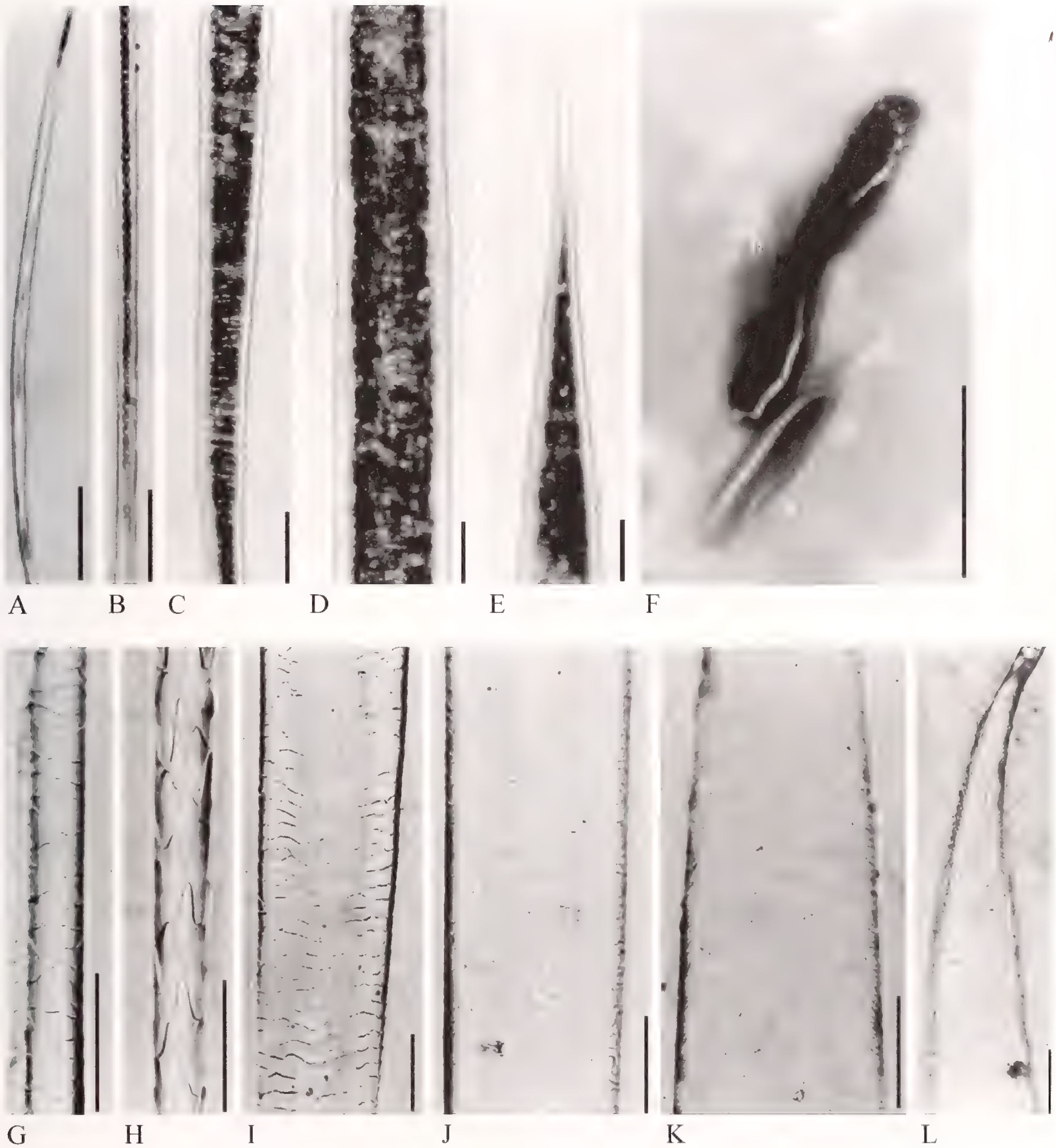

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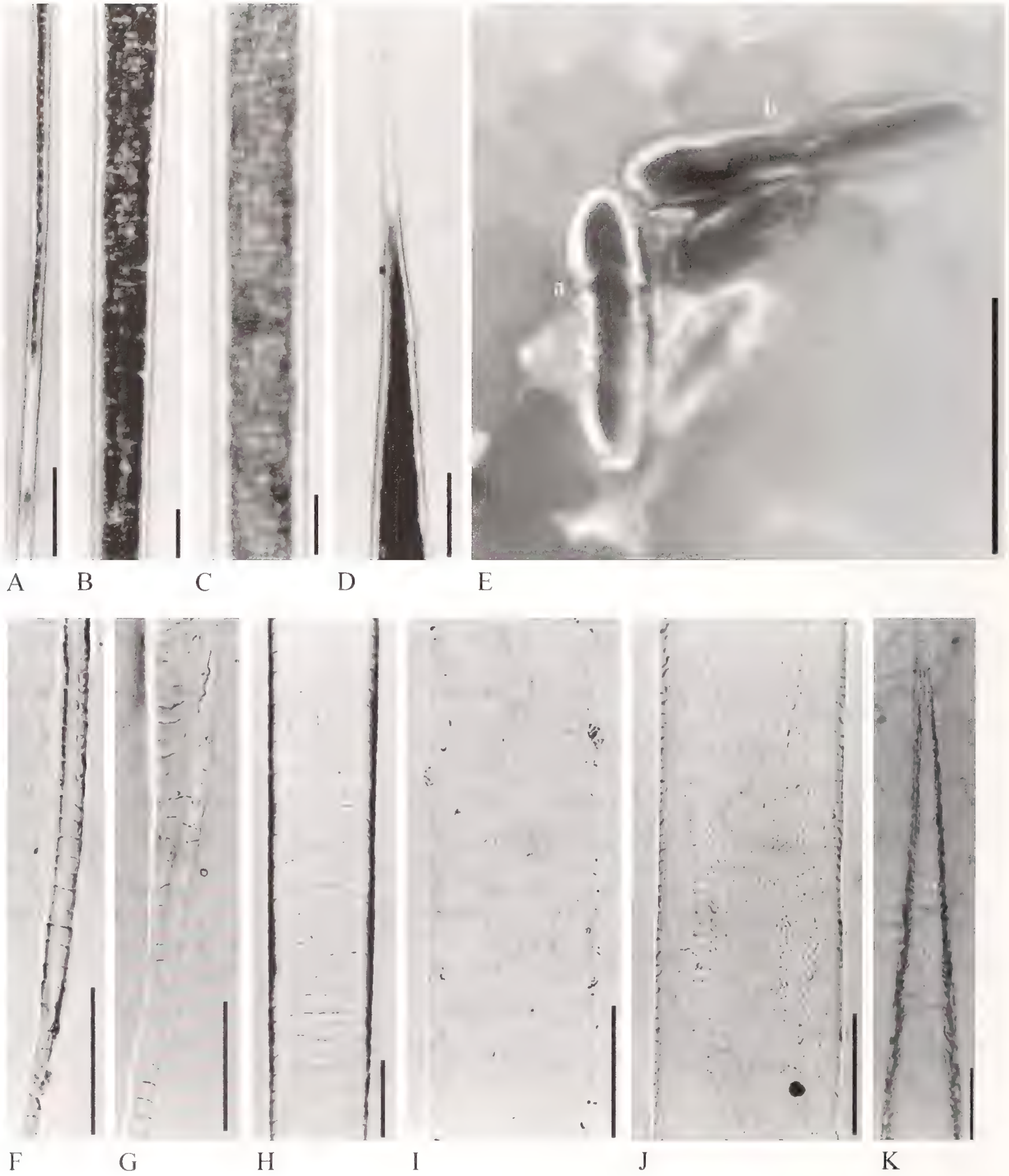

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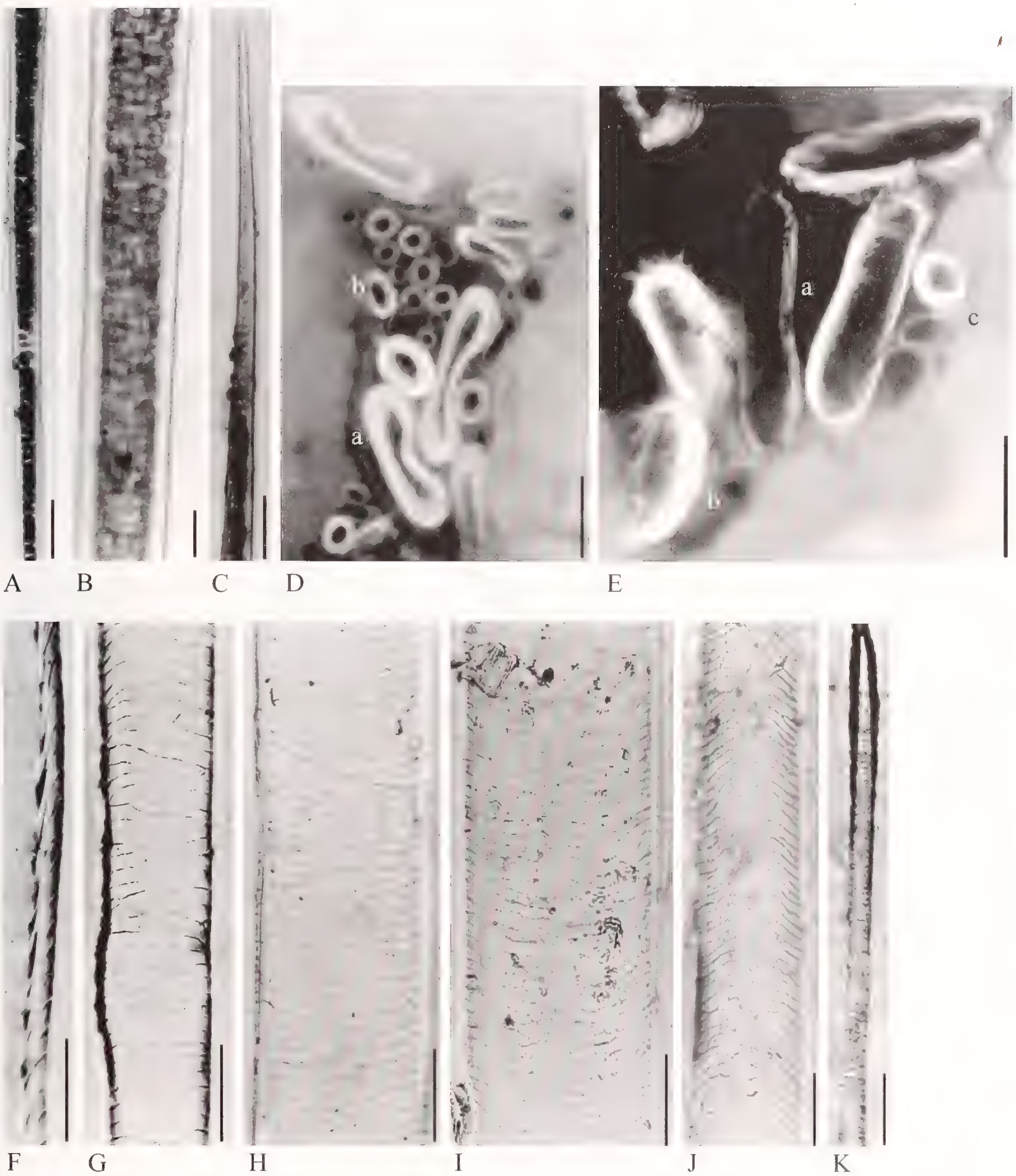

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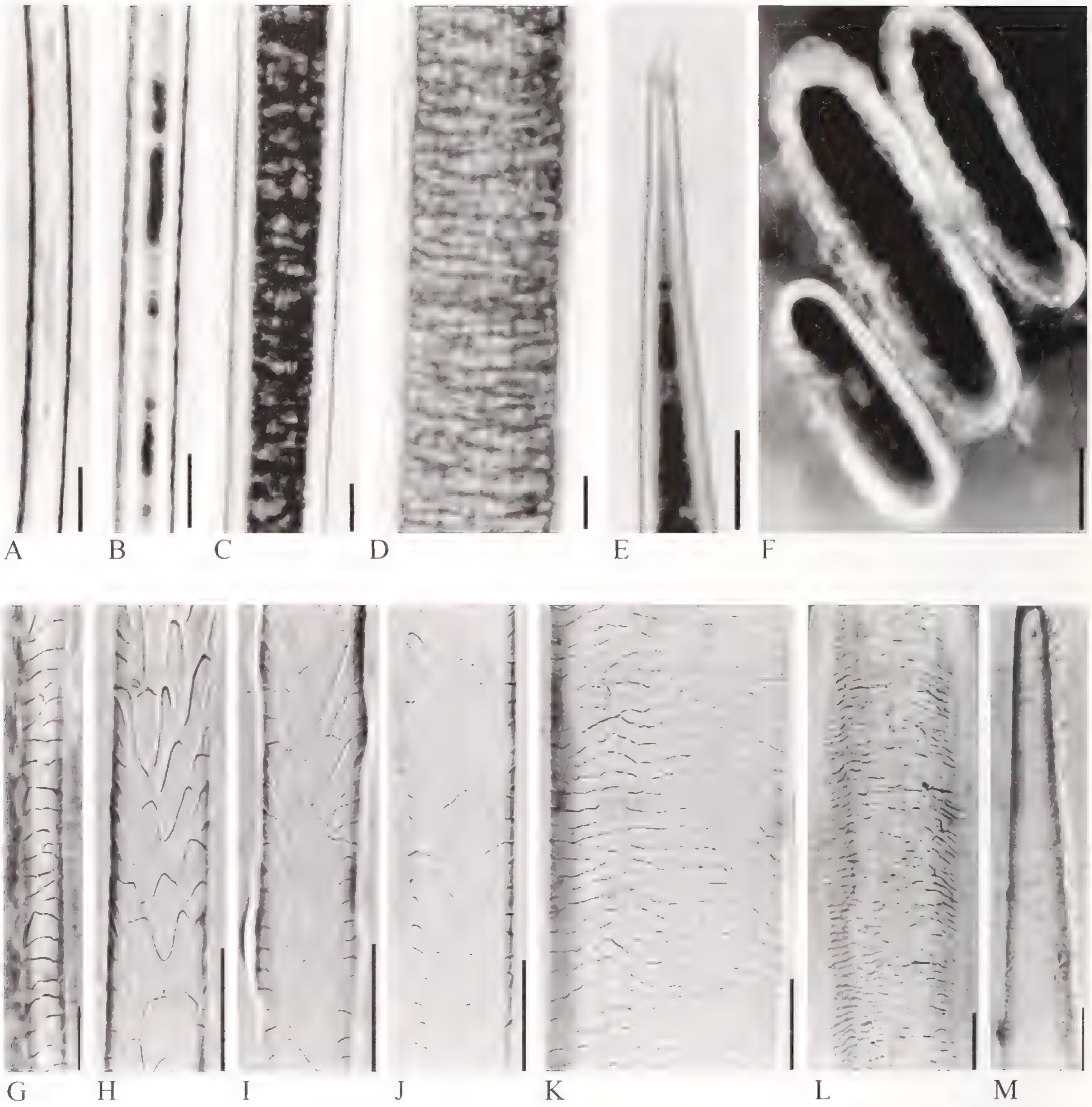

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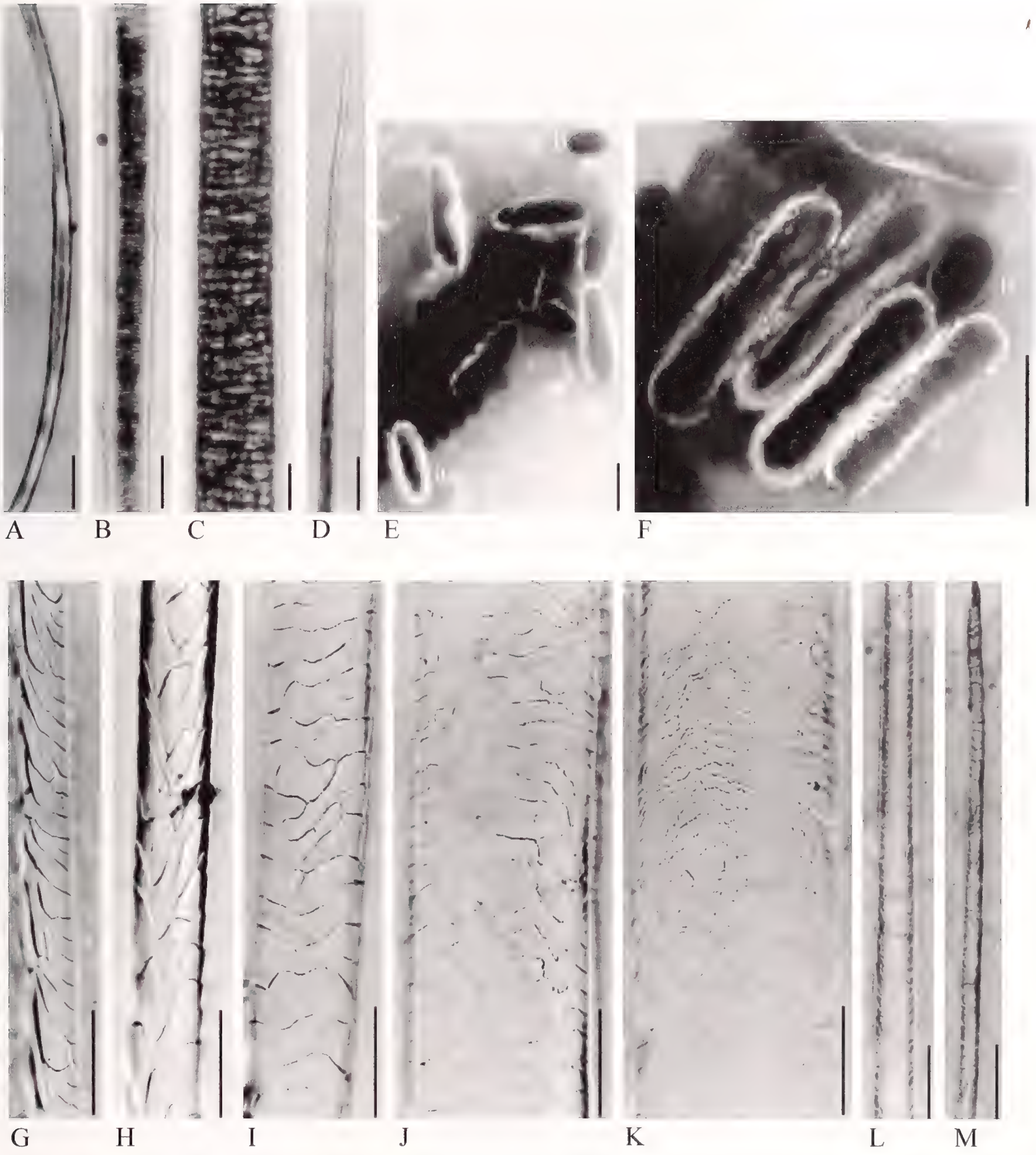

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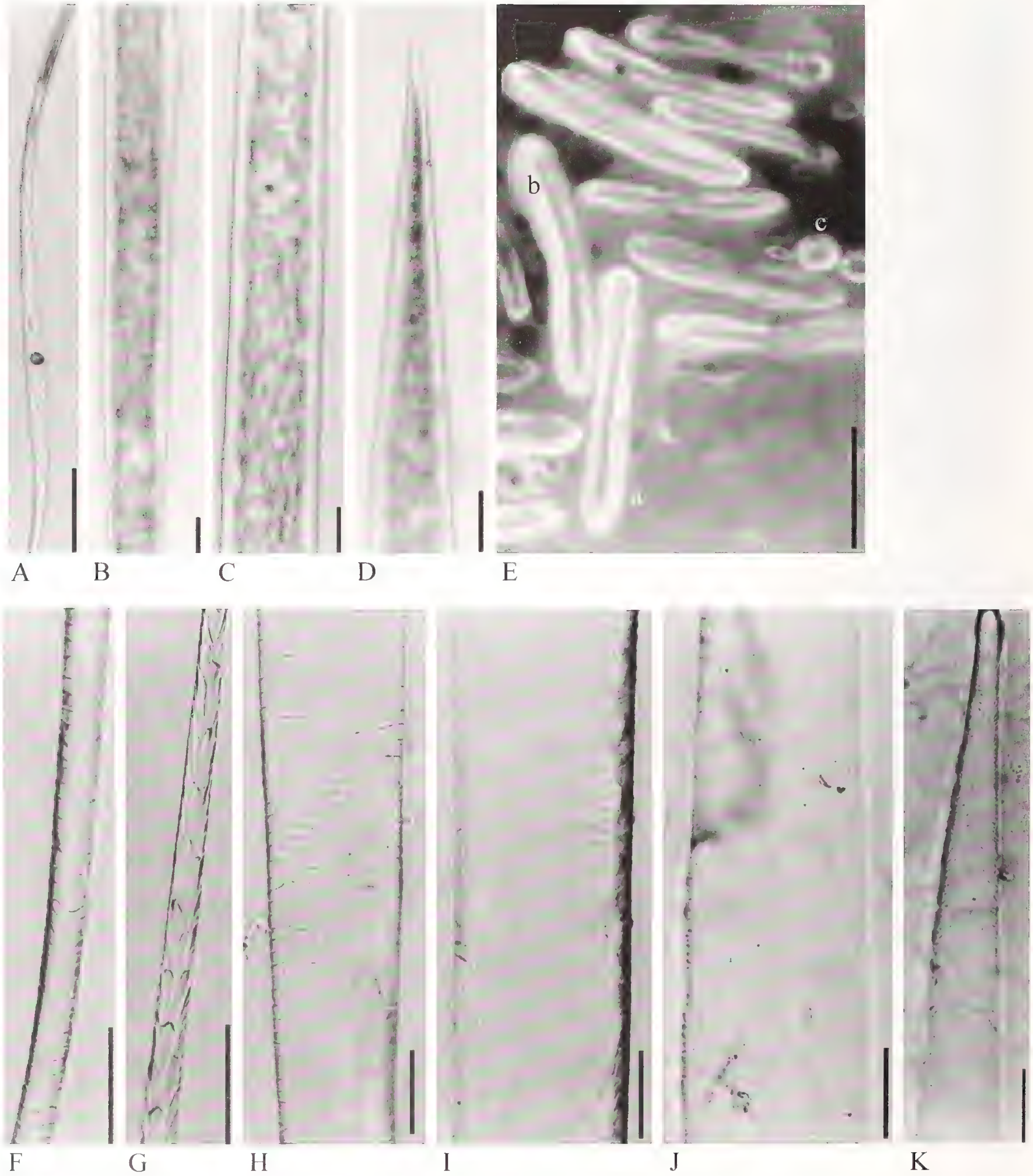

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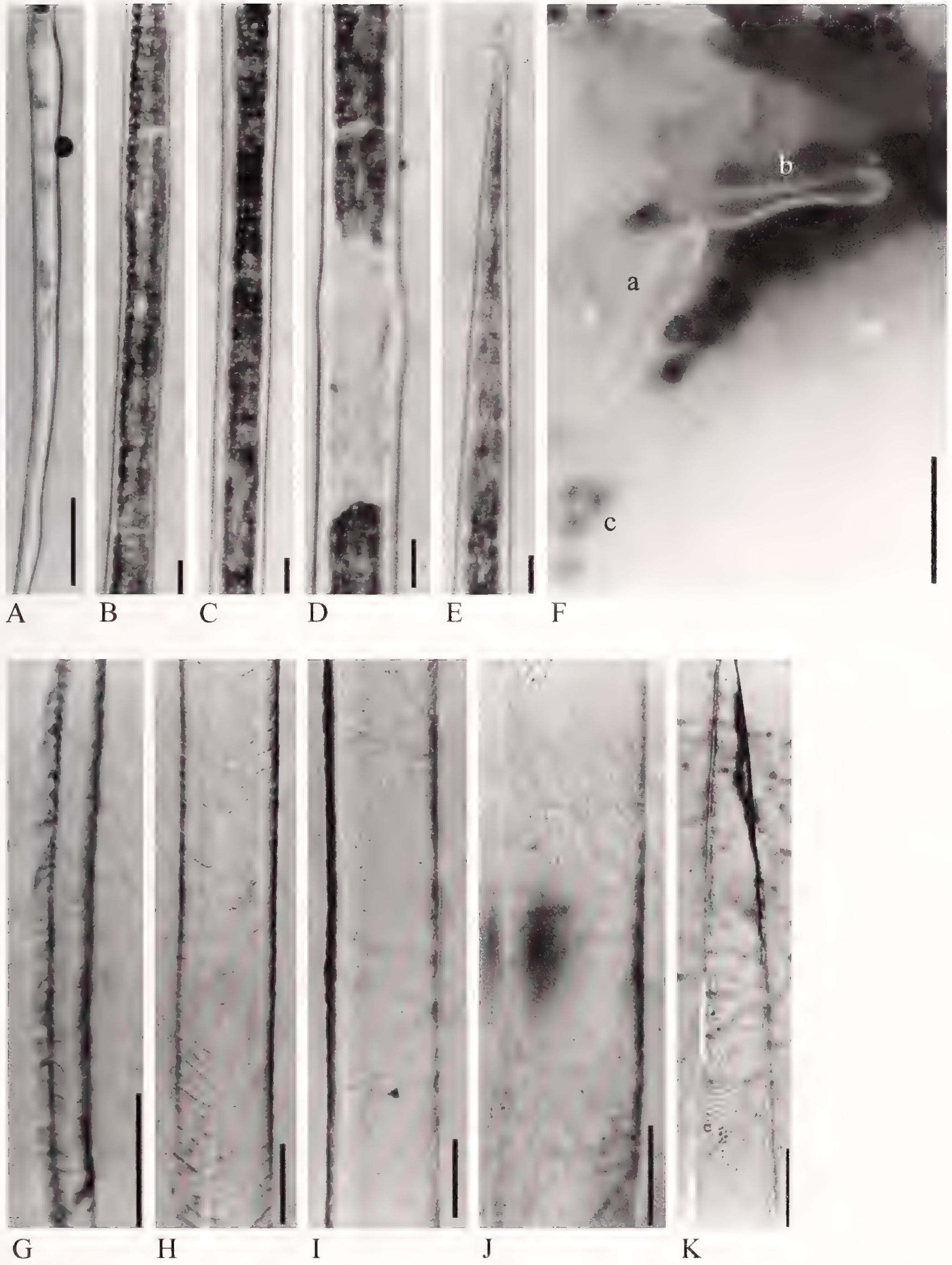

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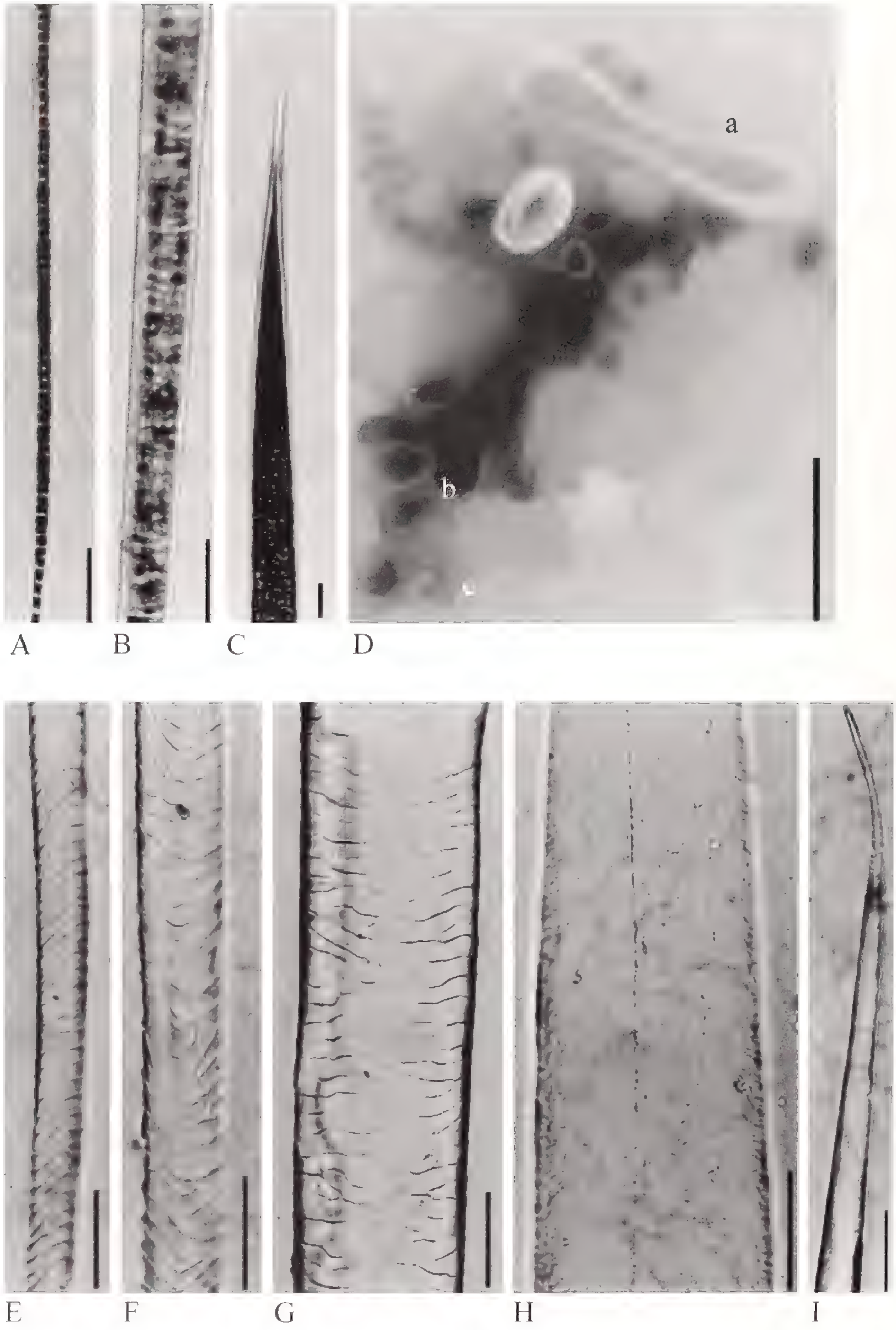

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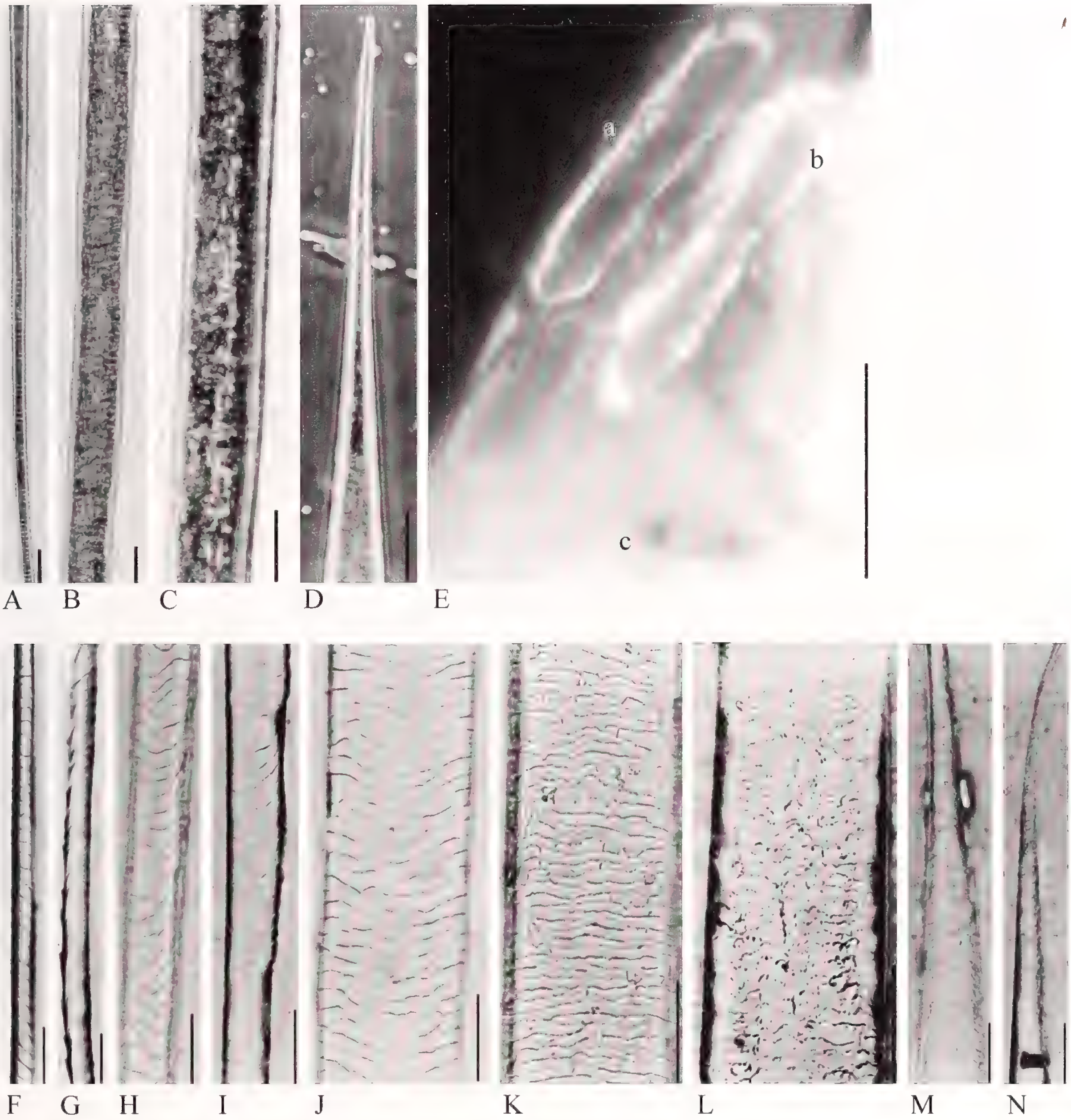

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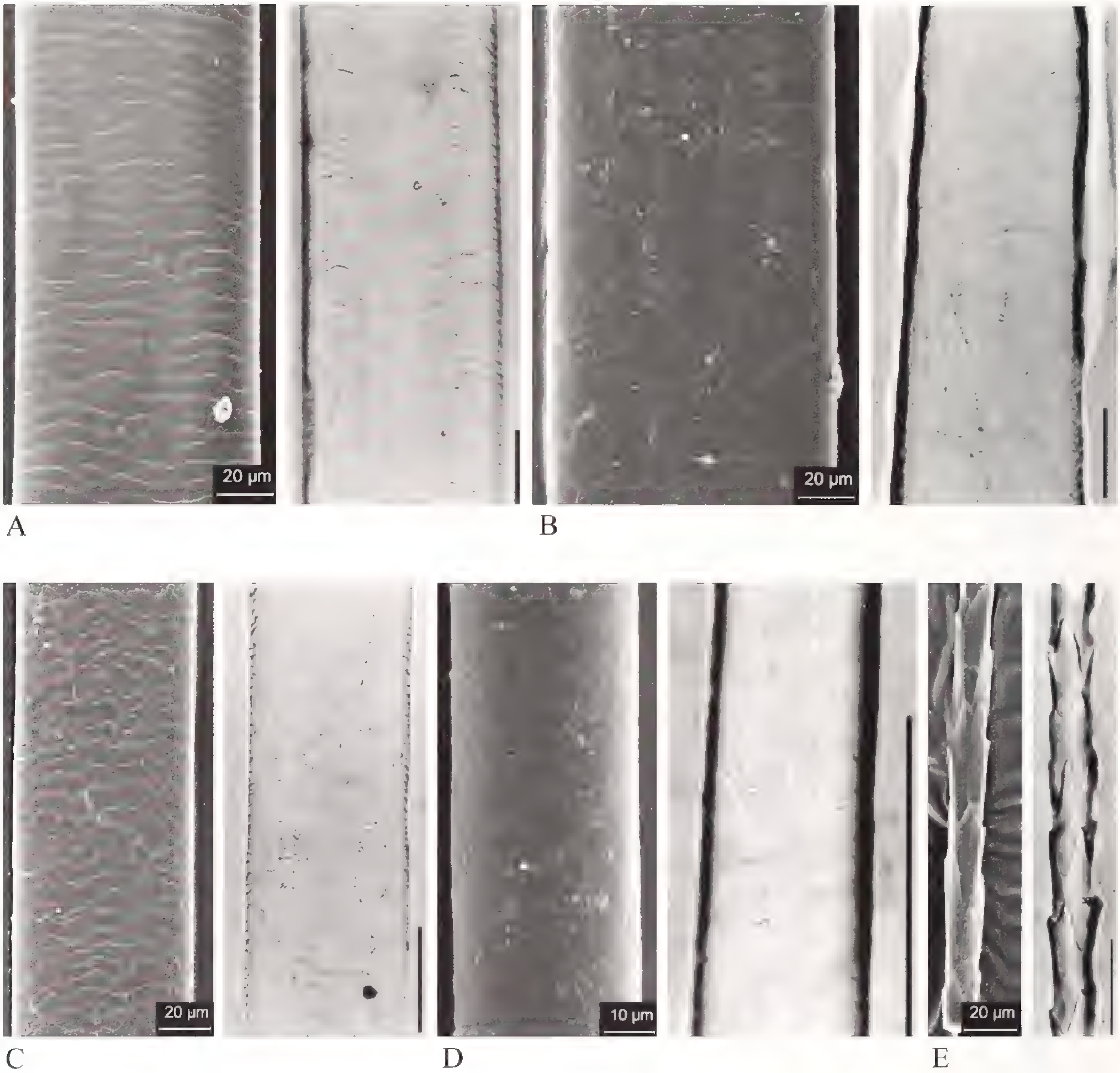

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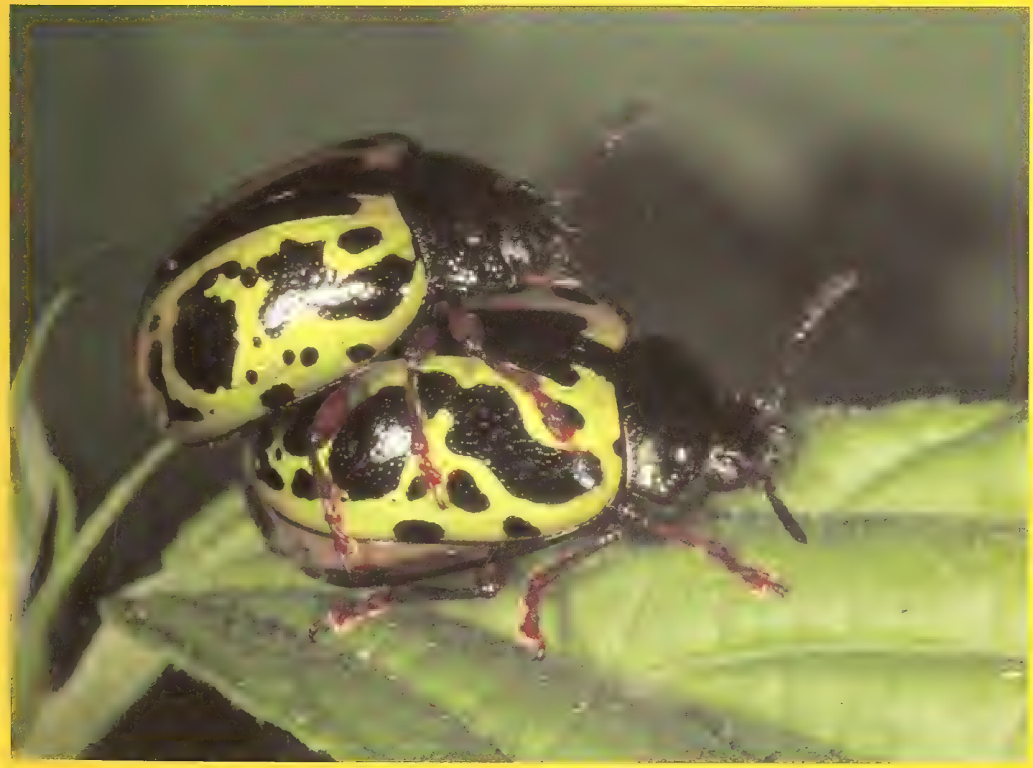

Band
54
Heft 4
2006 (2005)

Leibniz
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Bonner zoologische Beiträge werden publiziert im Eigenverlag Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn (Germany)

Die Zeitschrift erscheint mit vier Heften im Jahr, zum Preis von 11,50 € je Heft bzw. 46,- € je Band incl. Versand. Korrespondenz betreffend Abonnement, Kauf oder Tausch bitten wir zu richten an die Bibliothek, Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn (Germany). E-mail: d.steinebach.zfmk@uni-bonn.de.

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ISSN 0006-7172

Druck: Druck Center Meckenheim

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No. 1/2: 30. April 2006, No. 3: 30. August 2006, No. 4: 30. October 2006

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Biological Aspects of *Galeruca circassica* Reitter, 1889 (Coleoptera: Chrysomelidae: Galerucinae) in Relation to the Weed *Cephalaria procera* Fish. and Lall. (Dipsacaceae) in Anatolia[1]

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[2)] Nieuwegein, The Netherlands

Abstract. Biological aspects of *Galeruca circassica*, a herbivore feeding on *Cephalaria procera*, were studied in Turkey. In the laboratory, adults oviposited on *Cephalaria procera* from 9 days after emergence and laid an average of 198 eggs per female. Development of eggs and larvae proved to be temperature dependant. Larvae passed through four instars and pupated in a pupal case in the soil. Pupal stage lasted 48 days. Laboratory tests indicated that this species can complete its development on several *Cephalaria* species and on *Salvia staminea* and *Centaurea solstitialis*. Only on *Cephalaria procera* and *C. hirsute* a substantial percentage reached the adult stage. *Galeruca circassica* should be preserved in Eastern Anatolia because it most probably contributes in regulating the abundance of *Cephalaria procera* and because it might be used in biocontrol. The biology and host specificity of *G. circassica* indicates that it has a potential to be an agent for the biological control of *C. procera* in situations where this plant species occurs as an invasive plant.

Key words. Chrysomelidae, leaf beetle, *Galeruca circassica*, *Cephalaria procera*, biological control, weeds

1. INTRODUCTION

Cephalaria procera Fisch and Lall., 1840 (Dipsacaceae) is distributed in North Iran, Armenia and Turkey (DAVIS 1972). It is a perennial plant with subglabrous or sparsely pilose stems up to two meters. The flowers are pale yellow or cream. *Cephalaria procera* is very close to *C. gigantea*, possibly it has to be reduced to a subspecies of *C. gigantea* (DAVIS 1972). The Turkish name of *Cephalaria procera* is "Gevrek". *Cephalaria* plants root deep and the roots are strong which can be problematic in cultivating the ground (ploughing). In Eastern Anatolia "Gevrek" is regarded an important weed in meadows and pastures. Therefore a study was conducted of one of the herbivorous species associated with this plant and attempts were made to determine the influence of this species on *Cephalaria.*

Cephalaria is associated with several leaf beetle species. MEDVEDEV & ROGINSKAJA (1988) mention *Galeruca pomonae* (Scopoli) and *G. tanaceti* (L.) (Galerucinae) as polyphagous species feeding on *Cephalaria.* DOGUET (1994) mentions the polyphagous *Longitarsus luridus* (Scopoli) (Alticinae) feeding on *Cephalaria mauritanica* in Northern Africa and *Cephalaria syriaca* in Israel. In Turkey *Galeruca* is the only leaf beetle genus associated with *Cephalaria* (ASLAN pers. obs.).

The subfamily of Galerucinae comprises six tribes and approximately 5800 species (WILCOX 1971-1975) distributed throughout the world but predominantly in the tropics. In Turkey, this subfamily is known with 14 genera and 52 species (ASLAN 1998; ASLAN et al. 2000). In this subfamily, larvae feed on leaves or on plant roots in the soil, rarely on fruits. The biology of most species in this subfamily is unknown, except for the biology of pest species such as *Agelastica alni* (L.), *Aulacophora foveicollis* (Lucas) and *Xanthogaleruca luteola* (Müller) (ASLAN et al. 2000). On the other hand, there have been some attempts to study the biology of *Galerucella calmariensis* (L.) and *G. pusilla* in order to use them as biocontrol agents for management of *Lythrum salicaria* in the United States and some other countries (MCFAYDEN 1998).

The genus *Galeruca* is represented in Turkey by approximately 10 species (ASLAN et al. 2000). The genus is currently revised (BEENEN 1999, 2002, 2003) and possibly this will affect the number of Turkish species.

2. MATERIAL AND METHODS

2.1. Taxonomy

The specimens of *Galeruca* observed in this study belong to the *Galeruca pomonae*-group. From this species-group ASLAN et al. (2000) include *G. fuliginosa* (Joannis) and *G. pomonae* in their preliminary list of Turkish species. The inclusion of *G. fuliginosa* is based only on the type specimen collected in "Grece et Caucase". BEENEN (1999) concluded that *G. fuliginosa* is to be treated as a junior synonym of *G. littoralis* (F.) and that it is unlikely that it has been captured in the Caucasian mountains. The other species, *G. pomonae*, is a widely distributed and variable species. Many local forms have been described as different species and subsequent authors have synonymised these with *G. pomonae*. One of these, *G. circassica* Reitter, has been synonymised with *G. pomonae* by IABLOKOFF-KHNZORIAN (1968). ASLAN (1998) followed IABLOKOFF-KHNZORIAN in this respect. BEENEN (2005) gives arguments to remove *G. circassica* from synonymy and re-established it as a valid species. The results presented in the next paragraphs are based on the study of Turkish specimens of *G. circassica*.

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[1] Paper included here, but not presented to the 6th International Symposium on the Chrysomelidae, Bonn, Germany, May 7, 2004.

2.2. Development

Adults and larvae of *G. circassica* were collected from Gölyurt Pass (İspir, Erzurum), Olur (Erzurum) and Aşkale (Erzurum). The altitudes in the localities differed between 1000 m. and 2450 m. The collected specimens were used to start laboratory studies. Larvae and adults were placed in cages (50 x 45 cm) and kept at 20 (± 3) ^{0}C and 45 (± 10) % humidity. Fresh leaves of *Cephalaria procera* taken from the same localities were placed in the cages. In order to keep the leaves fresh their petioles were dipped in glass vials (15 ml) filled with tap water. The leaves were replaced every four days. The bottom of the cages was covered with a layer of soil (three cm) in which larvae could pupate. Cages with pupal cases were retained in laboratory, under natural photoperiod (during July approximately 12 hours dark). Eggs were removed every 24 hours.

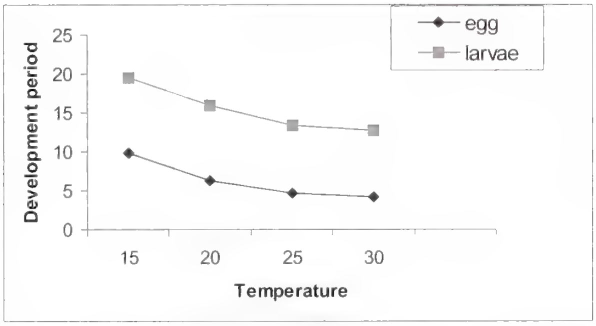

Fig. 1. Development period of larvae and egg in different temperature.

To determine the effect of temperature on egg development, eggs less than 24 hours old were placed, still attached to *C. procera*, on moist filter paper in petri dishes in each of four constant environment chambers at 15 ^{0}C (n= 25), 20 ^{0}C (n= 25), 25 ^{0}C (n=25) and 30 ^{0}C (n=25) (RH 65 ± 5 %; 12h L: 12 h D). Twice every day, at 8:30 and 19:30, newly hatched larvae were counted and removed.

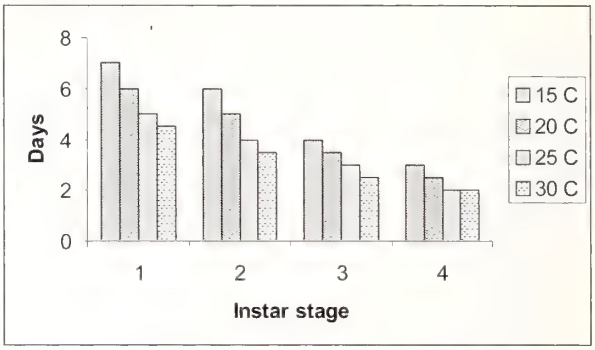

Fig. 2. Days taken for each instar stage to develop at 15, 20, 25 and 300C.

To determine the effect of temperature on larval development newly hatched larvae were kept in constant environment chambers at 15 ^{0}C (n= 20), 20 ^{0}C (n= 20), 25 ^{0}C (n=20) and 30 ^{0}C (n=20) (RH 65 ± 5 %; 12h L: 12 h D). Each larva was placed on a fresh leave. In order to keep the leaves fresh their petioles were dipped in glass vials (15 ml) filled with tap water. Larvae were monitored twice daily at 8:30 and 19:30. Leaves were replaced every other day. After the final moult, the bottom of each cage was covered with soil as above.

2.3. Foodplants

In the province of Erzurum the vegetation was studied in Ispir, Pasinler, Olur, Aşkale and Oltu. Plant species of the genera *Cephalaria*, *Salvia*, *Centaurea*, *Cirsium* and *Scabiosa* were intensively examined for the presence of *G. circassica* eggs, larvae, and adults. Each plant species, regardless the number of individuals, was examined for 15 minutes.

In addition also laboratory tests were conducted. Five species of *Cephalaria* including *C. procera*, two species of *Centaurea* and *Salvia* and one species of *Cirsium* and *Scabiosa* were tested in no-choice tests for feeding.

Adults manually removed from pupal cases 25 to 35 days after pupation were used in tests for feeding. Six adults (3 males and 3 females) were placed on each leaf for the above mentioned species. In larval test three first instar larvae were placed on each plants leaf. In order to keep the leaves fresh their petioles were dipped glass vials filled with tap water. The leaves were replaced every four days. The no-choice tests were carried out in the laboratory under natural light condition at 20 ± 3 ^{0}C and a relative humidity of 45 ± 10%. All plants were tested separately using three replicates.

2.4. Predators and parasites

In the province of Erzurum, eggs, larvae and pupae were observed to identify possible predators or parasites. Additionally eggs, larvae and pupae were collected and placed in a cage for emerging parasites.

3. RESULTS

3.1. Development

Eggs of *G. circassica* were 1.9±0.015 mm (after the ± sign the standard deviation is indicated) long 1.5±0.005 mm (n=25) wide and deposited in groups at the underside, rarely at the upper side, of the leaves. Eggs were initially translucent to dirty white, becoming darker during development. Egg development took 9.8±0.17 (n=30), 6.3±0.14 (n=30), 4.7±0.08 (n=30), and 4.2±0.04 (n=30) days at 15, 20, 25, and 30 ^{0}C, respectively (Fig. 1).

Larvae emerged (head first) and immediately started feeding on the foliage. The black larvae passed through four instars, taking 19.5±0.17 (n=30), 16±0.14 (n=30), 13.4±0.11 (n=30) and 12.7±0.08 (n=30) days from emergence to the construction of the pupal case at 15, 20, 25, and 30 ^{0}C, respectively (Figs. 1, 2). Larval mortality was lowest at 20 ^{0}C and highest at 30 ^{0}C, especially during the first instar stage. Mature larvae dropped to the ground where they pupated in a pupal case in the soil.

In the laboratory 80.5 % (145/180) of the larvae that entered the pupal stage emerged as adults. Pupal stage lasted 47.8 (±1.86) days and was independent of temperature.

On the locations were field studies were conducted active *G. circassica* adults were present mainly from the beginning of May to the end of June. *Galeruca circassica* eggs and larvae were found on *C. procera* in from mid of May to the beginning of July.

3.2. Food plants

Eggs, larvae and adults of *G. circassica* were recorded in the field on plant species of the families Dipsacaceae, Lamiaceae and Asteraceae (Table 1). The highest presence occurred on plant species of *Cephalaria*, especially *C. procera*. *Salvia staminea* and *Centaurea solstitialis* were the only species in the subfamilies Lamiaceae and Asteraceae on which *G. circassica* were registered.

Table 1. Plant species monitored in the field in Turkey for presence of *G. circassica*.

Family	Species	Sites[a]	Occasions[b]	Present[c]
Dipsacaceae	*Cephalaria aristata*	10	5	2
	C. hirsute	20	12	12
	C. speciosa	15	10	3
	C. anatolica	13	8	2
	C. procera	48	115	45
	C. syriaca	12	12	4
	C. media	8	4	1
	C. gigantean	18	9	2
Lamiaceae	*Salvia staminea*	5	4	1
	S. verticillata	4	5	0
	S. brachyantha	3	2	0
Asteraceae	*Centaurea depressa*	8	9	0
	C. solstitialis	25	55	3
	C. iberica	11	5	0
	C. virgata	9	2	0
Asteraceae	*Cirsium arvense*	38	76	0
	C. ciliatum	5	3	0
Dipsacaceae	*Scabiosa rotata*	11	5	0
	S. columbaria	4	2	0

[a]Sites monitored; [b]Occasions each site monitored; [c]Sites *Galeruca circassica* present.

No-choice tests revealed that *G. circassica* laid eggs on all plant species on which this *Galeruca* species has been observed in the field. Most eggs were laid within nine days of the adults' removal from pupal cases. Each female deposited on average 198 eggs. Although intense feeding was observed on only one species (*C. procera* showing severe damage) many adults survived for 45 days on most species tested (Table 2). Larvae completed their development on *Cephalaria* spp. and two other species, *Salvia staminea* and *Centaurea solstitialis* (Table 2).

Table 2. Plant species tested in larval and adult no-choice test.

	Larvae			Adults			
Test plants	**n[a]**	**% Pupated[b]**	**Damage[c]**	**n[a]**	**%Alive[d]**	**Eggs[e]**	**Damage[c]**
Cephalaria procera	10	85	S	9	80	250	s
C. hirsute	8	50	S	5	78	175	M
C. arsistata	5	20	M	4	70	60	M
C. speciosa	5	10	M	5	72	20	NE
C. anatolica	5	8	M	2	69	18	NE
Salvia staminea	3	2	NE	1	67	32	NE
S. verticillata	3	0	N	0	60	0	N
Centaurea depressa	3	0	N	1	69	0	N
C. solstitialis	3	3	M	2	58	29	NE
Cirsium arvense	3	0	N	0	52	0	N
Scabiosa rotata	3	0	N	0	55	0	N

[a]Number of replicates; [b]Mean percentage of larvae for replicates reaching the pupal stage; [c]Estimated damage (N, none; NE, negligible; M, moderate; S, substantial); [d]Mean percentage of adults alive for all replicates after 45 days; [e]Total number of eggs laid after 45 days.

3.3. Predators and parasites

In this study no natural enemies were found that were associated with *G. circassica*. However, one Miridae (Heteroptera) species, *Deraecoris seranus* Dgl, was seen feeding on the eggs of *G. circassica*, but their density was low. On the other hand, this species is zoophytophagous and feeds generally on alfalfa, some other cultivated plants and weeds.

From eggs, larvae or pupae no parasites emerged.

4. DISCUSSION

Life history tables of species of *Galeruca* (subgenus *Galeruca*), as far as known, show some remarkable similarities. The minor differences seem to be related to the exact months of summer heat and severity of winter. In the North-western part of its distribution *Galeruca pomonae* shows adult aestivation during summer (July and August) and reproduction in late summer and autumn (from September to the end of October) (BEENEN 1998). In Sardinia *Galeruca sardoa* (Gené) show summer aestivation from the end of June to the start of October. Reproduction takes place from November to January (CROVETTI & USCIDDA 1978.). In Sicily *Galeruca* species (*G. sicana* (Reiche) and *G. reichei* (Joannis)) show summer aestivation during July and August and reproduction from September to December (SINACORI & MINEO 1993). All these species show egg diapause during winter. The life history of *G. circassica*, a species hitherto confused with other *Galeruca* species, is unknown. The results of this study however show remarkable differences with the above mentioned species. *Galeruca circassica* is known to overwinter in the adult stage, mate and deposit eggs in spring and completely develops during early summer. From this study it became clear that development takes place in approximately 70 days. Eggs were seen in the field from mid May onwards, consequently adults could be seen some 70 days later: from the end of July. The results from the laboratory studies fit the results from the field. Adults of *G. circassica* overwinter and reproduce in spring. This life history table is in concordance with the observations on *Galeruca rufa* Germar by BOURDONNÉ & MALDÈS (1995). In the south of France *Galeruca rufa* deposits eggs from mid May to the end of August. Larvae are active during summer. Adults can be seen almost all year. *Galeruca rufa* is not related to *Galeruca circassica*. It is classified in the subgenus *Emarhopa*; *G. circassica* in the subgenus *Galeruca*.

From eggs, larvae or pupae no parasites emerged. Only a single predator has been observed. Most probably this subject needs some additional research. Other *Galeruca* species are known to be parasitized by Hymenoptera and Diptera parasites (COX 1994) and predated by *Zicrona* (Heteroptera), *Lebia* (Carabidae) and *Aiolocaria* (Coccinellidae) (COX 1996). It is unlikely that *Galeruca circassica* has no parasites.

The distribution of *G. circassica* is insufficiently known due to the taxonomic entanglement. This study provides information on the occurrence in eastern Anatolia. The description of *G. circassica* was based on specimens collected in Fisht in the north-western part of the Caucasian mountain range (REITTER 1889). Further study of collections and surveys in the field must provide knowledge about its distribution.

Food plants of *G. circassica* mentioned in literature are not reliable because of the uncertain taxonomic position of this species. The same may hold true for *G. pomonae*. Records of *G. pomonae* from the Caucasian area could refer to *G. circassica*. GRUEV & TOMOV (1986) and WARCHAŁOWSKI (1994) indicate that *G. pomonae* could feed on *Centaurea, Salvia, Knautia, Cirsium*, and *Scabiosa*. MEDVEDEV & ROGINSKAJA (1988) mention *Mentha* and *Melissa* as possible (marked with question mark) food plants for *G. circassica*. These authors mention *Cephalaria* as food plant for *G. pomonae*.

The observation in our study show that *G. circassica* feeds primarily on *C. procera* and *C. hirsute*; plants which are widespread and abundant in eastern Anatolia. These plants are important weeds and *G. circassica* most probably contributes in regulating their abundance. However, because both *Cephalaria* and *G. circassica* are indigenous in this region it is unlikely that *G. circassica* will control this food plant completely. In situations were *Cephalaria* is introduced and causes problems, the possibility of using *G. circassica* as a biological control agent should be seriously investigated. Our study revealed that both adults and larvae of *G. circassica* feed on *C. procera* and cause important damage.

In Anatolia a decline of *G. circassica* (e.g., a decline due to the use of non-specific insecticides) should be prevented because this leaf beetle can help in restricting the nuisance caused by "Gevrek". Furthermore it is a potential agent for the biological control of *Cephalaria* in other places.

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Bonner zoologische Beiträge	Band 54 (2005)	Heft 4	Seiten 179–199	Bonn, Oktober 2006

Translocation in Leaf Beetles (Coleoptera: Chrysomelidae)[1]

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Abstract. An overview of leaf beetle translocations, and the possible effects related to endangerment of native leaf beetle species is presented. Translocation is defined as the movement of living organisms from one area to another across natural barriers. In the new area the translocated organism lives free. Translocations can be intentional or accidental. The database of records of translocated leaf beetles is compiled using published records as the main source of information. In this study 126 leaf beetle species have been recorded to have been translocated at least once. Most translocated species occur in the subfamilies Chrysomelinae, Galerucinae, Alticinae, Cassidinae and Hispinae. Most unintentional successful translocations occur in mono- and oligophagous species that develop on cultivated and non-indigenous plant species. At present, no negative effects of translocated Chrysomelidae on biodiversity have been reported. The successful control of imported weeds by introduced Chrysomelidae can be seen as a positive effect to biodiversity since some of these weeds prevent natural processes in ecosystems. Historical distribution patterns of Chrysomelidae are discussed in relation to the translocations.

Keywords. Coleoptera, Chrysomelidae, invasive species, bioinvasion, alien species, translocation, introduction

1. INTRODUCTION

One of the major threats to native biological diversity is now acknowledged by scientists and governments to be biological invasions caused by alien invasive species (IUCN 2000, UNION OF CONCERNED SCIENTISTS 2001). This is not a new item: the threat of invasive species for the conservation of biodiversity was already pointed out by ELTON in 1933 (cf. SIMBERLOFF's foreword in ELTON 2000). Meanwhile it is supposed that every year a wide range of alien species are imported into many countries through international trade both intentionally as trade products (horticulture, pets, etc.) or unintentionally (for example by hitch-hiking on legitimate products). Little is known about the number of leaf beetles (Coleoptera, Chrysomelidae) that are translocated in this way or about their impact on biological diversity.

Translocated species can be a threat in the way that a native leaf beetle is displaced by an alien leaf beetle species. On the other hand translocated species can reduce indigenous plant species and thus affect the native herbivores depending on it. In this study we restrict consideration to leaf beetle translocations and their effects on native leaf beetle populations caused by competition.

Interspecific competition is any interaction between two or more species populations which adversely affects their growth and survival (ODUM 1971). The importance of interspecific competition is not clear (STEWART 1996) but evidence for competition among phytophagous species (including Chrysomelidae) exists (e.g., GONZÁLES-MEGÍAS & GÓMEZ (2003)).

When a population of a non-indigenous species out competes a population of a native species, the invasive species must have reached a population level in which its competition can be effective. When the population level is too low, it is unlikely that there will be a large effect on the population of the indigenous species. COLAUTTI & MACISAAC (2004) developed a framework for defining different stages during invasions. After the new species is established a non-indigenous species may be localised and rare (a), widespread but rare (b) or widespread and dominant (c). In this last mentioned stage, out competing of indigenous species may be the result.

Therefore, for our purpose, we need to know whether translocated Chrysomelidae have become established. That is the first step. Subsequently we would like to know the status of the established species. The aim of this study is to get an overview of leaf beetle introductions, and the possible effects related to endangerment of native leaf beetle species.

Natural range expansion of a species, as for example recorded for *Chaetocnema major* Jacquelin-Duval by DÖBERL (1994a), is not treated here. Here we consider all transport across natural barriers as translocation. Both intentionally (e.g., in biological control programs) as unintentionally. The IUCN (1987) defines translocation more strictly and restricts to "introductions", "re-introductions" and "re-stocking". Introductions can be effective tools in the management of natural and man made environments. Re-introduction and re-stocking as an aim in nature management has not been used with

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[1] Paper presented to the 6th International Symposium on the Chrysomelidae, Bonn, Germany, May 7, 2004.

Chrysomelidae species. Thus, for this purpose we do not have to include the IUCN-restrictions.

Here we define translocation as the movement of living organisms from one area to another across natural barriers. In the new area the translocated organism lives free. Translocations can be intentional or accidental. The role of man is not always clear in cases of translocation.

2. METHODS

The database of records of intentionally or non-intentionally introduced leaf beetles is compiled using published records as the main source of information. Because not all published information was available for this study there is a chance that information is lacking; this is believed to be compensated by other publications in which similar information is available.

Only the traditional leaf beetles have been studied, i.e. exclusive the Bruchidae. Subfamily names used in this study are the traditional as have been used by SEENO & WILCOX (1982). All species group names of Chrysomelidae in Appendix 1 are scientific names complete with author. In the text they are without author names, except for those species that are not listed in Appendix 1.

A translocation event is defined as a translocation from an area where the species is indigenous to an area where the species previously did not occur. In this respect the translocation of *Chrysolina hyperici* from England to Australia in 1930 and from France to Australia in 1980 are considered as two different translocation events. In the case of biocontrol, translocations with different targets (host plants) are considered as different translocation events.

Excluded from the database are natural expansions. However we have to admit that it is not always clear to discriminate between natural range expansion and transport across natural barriers. This might be the case in species that are still in the phase of post-glacial expansion.

Also accidental translocations that have resulted in establishment in artificial environments as in greenhouses are not included in this research. In the Netherlands for example the alticine *Acrocrypta purpurea* Baly has established in a greenhouse where during several generations it damaged orchids (DÖBERL 1994b). *Acrocrypta purpurea* originates from South East Asia and it is unlikely that it will survive in the Netherlands outside (green)houses.

Sometimes it is difficult to define the exact moment of establishment. *Leptinotarsa decemlineata*, for example, was discovered in the Rocky Mountains and described in 1824. Suddenly, in 1859, it began devastating potato crops 100 miles west of Omaha, Nebraska, USA. Over the next few years, the beetle spread eastward to the Atlantic coast, which it reached in 1874. *Leptinotarsa decemlineata* became established in Europe following its introduction from the USA to Bordeaux, France in 1922 (after several unsuccessful attempts from 1876). The beetle spread rapidly in Europe despite intensive operations to control it. It was first reported in Belgium and Spain in 1935, Luxembourg in 1936, the Netherlands and Switzerland in 1937, Austria in 1941, Hungary and the former Czechoslovakia in 1945, Poland and Romania in 1947, and Turkey in 1949 (CAB-CPC 2003). In Appendix 1 the year 1922 is taken as the moment of establishment in Europe although it has been found earlier in France and established many years later in some European countries.

On the other hand a species may not have established in all parts of the country to which it is translocated. For example: all attempts to establish *L. jacobaeae* in Ontario, New Brunswick and Prince Edward Island were unsuccessful. In Canada it is at present established only in British Columbia. In the United States it is currently known from California and Oregon (LESAGE 1988).

3. RESULTS

In this study 126 leaf beetle species have been recorded to have been translocated at least once. They are listed in Appendix 1. Because many species have been translocated more than once, a total number of 230 translocation events in Chrysomelidae is listed (Appendix 1). Of each event information is given on place of origin of the leaf beetle, place where it is translocated to, moment of translocation, degree of success, host plant and source (reference). In Figure 1 the length of each bar represents the total number of species of each subfamily. Most translocated species occur in the subfamilies Chrysomelinae, Galerucinae, Alticinae, Cassidinae and Hispinae. In Figure 2 the length of the bar represents the number of translocations of each subfamily. The bar for the subfamily Hispinae is much larger than in Figure 1, indicating that some species have been translocated several times.

Translocations can be intentional or unintentional. The number of intentional translocations exceeds the number of unintentional translocations (Table 1). This is not surprising. Unintentional translocations are hard to detect; they mostly have not been published. Publications on species that have been unintentionally translocated mostly will deal with species that have become established in the newly inhabited land. When established they are more likely to be observed. Of the unintentional translocated species 81 % (70 out of 86) have become established against 63 % (91 out of 144) of the intentionally translocated species. The successes of intentional translocations that are part of a biological control program are monitored. This means that not only information on successful translocations are available but also of the unsuccessful releases. On the other hand the intentional translocations mostly take place only after intensive study. In biological control programs the success (and the risk) of the introduction is carefully studied before release. In that respect it is surprising to notice that 27 % (39 out of 144) of the intentionally translocated species have not become established.

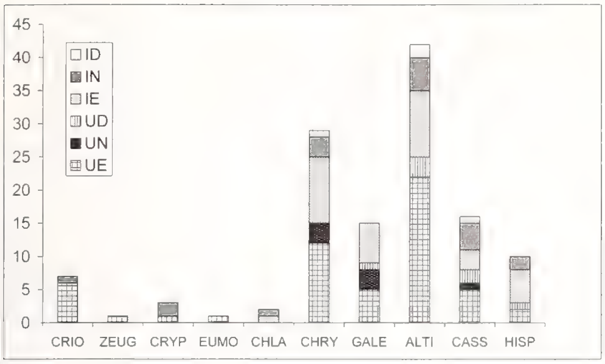

Fig. 1. Results of translocations in Chrysomelidae. Number of translocated species per subfamily. Subfamily abbreviations: CRIO = Criocerinae; ZEUG = Zeugophorinae; CRYP = Cryptocephalinae; EUMO = Eumolpinae; CHLA = Chlamisinae; CHRY = Chrysomelinae; GALE = Galerucinae; ALTI = Alticinae; CASS = Cassidinae; HISP = Hispinae. Results: UE = unintentional translocation followed by establishment; UN = unintentional, not established; UD = unintentional, establishment doubtful; IE = intentional and established; IN = intentional and not established; ID = intentional and doubtful.

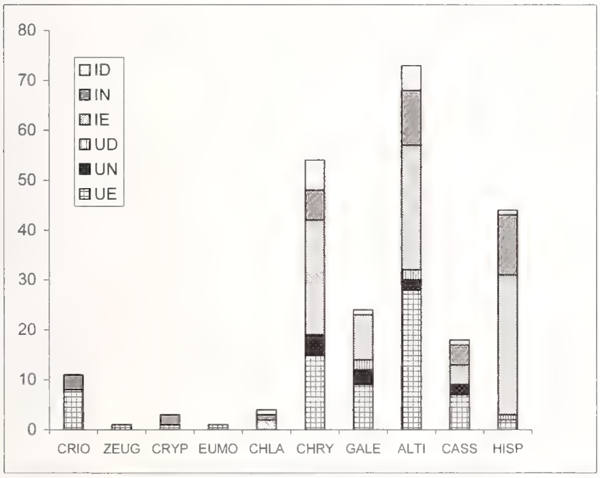

Fig. 2. Results of translocations in Chrysomelidae. Events per subfamily. Subfamily abbreviations as in Figure 1. Results: UE = unintentional translocation followed by establishment; UN = unintentional, not established; UD = unintentional, establishment doubtful; IE = intentional and established; IN = intentional and not established; ID = intentional and doubtful.

Intentionally translocated species mostly have very restricted food preference. The chances that they become a problem as a result of feeding on non-target species is lowest in monophagous species. We analysed the food preference of the unintentionally translocated species. In Figure 3 the number of species is presented for the next groups of phytophages: monophages – species that develop on a single plant species or genus; oligophages – species that develop on more than one plant genus of a single plant family; polyphages – species that develop on plant species of more than one family. It shows that most of these successful translocated species are mono- or oligophagous; they develop on plant species within a single genus or within a single plant family. This more or less implies that, because of the food restriction of most leaf beetles, host plants from the same genus or family have to be available in the new country.

It is interesting to find out what types of plants these successfully unintended translocated species feed on. Four categories of plants species have been distinguished: cultivated plant species, non-indigenous "wild" plants, indigenous "wild plants" and a last category of which information was insufficient (Fig. 4). It is evident that the majority of unintended successful translocation of leaf beetles occurred on cultivated plants and on non-indigenous (introduced plant species). Only a minority occurs on plants that are indigenous.

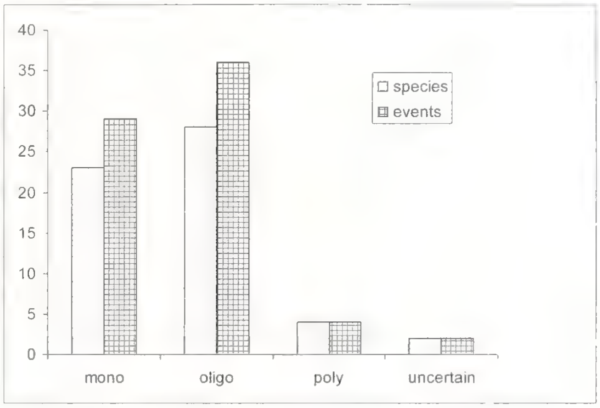

Fig. 3. Number of unintentionally translocated leaf beetles that have established per categories of food plants. Mono = monophagous, oligo = oligophagous, poly = polyphagous. Species = number of translocated species, events = number of translocation events.

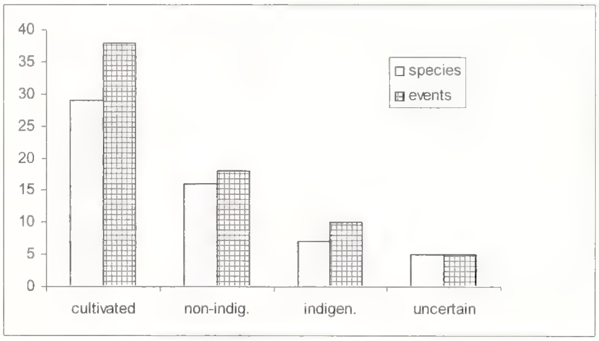

Fig. 4. Number of unintentionally translocated leaf beetles that have established per plant category: cultivated plants, non-indigenous plants, indigenous plants and plants of which this information is not available.

4. MISCELLANEOUS RESULTS

Apart from the results described above, interesting information became available on a variety of subjects. An extract of this is presented in this section. The following subjects are presented: description of species based on translocated specimens; unused biological control agents; the use of indigenous species in biological control; anecdotal information on the ways unintentional translocations have taken place and finally non-target effects.

4.1. Description of species based on translocated specimens

Some species description were based on displaced specimens: *Falsoplatyxantha diversicornis* Pic, *Luperus marginalis* Allard and *Aulacophora pannonica* Csiki (= *Hoplasoma unicolor* Ill.) (all Galerucinae). The type specimen(s) of *Falsoplatyxantha diversicornis* were from Turkey, but the author already stated that the species most probably originally came from the Indies ("Acquis comme provenant d'Asie Mineure, mais originaire vraisemblablement des Indes") (Pic 1931). Of *Hoplasoma unicolor* a single specimen was collected in Hungary and described as *Aulacophora pannonica* by Csiki (1953). Silfverberg (1978) studied the type specimen of *A. pannonica* and reduced it to a junior synonym of *H. unicolor*. The type specimen of *A. pannonica* was probably imported from the Oriental region. Although there always remains the possibility of mislabelled specimens (see Mohamedsaid 2001). *Luperus marginalis* was described by Allard (1890) from the Falkland archipelago and according Jolivet & Verma (2002) evidently imported there in historical times. Apart from *L. marginalis* no Chrysomelidae have been mentioned from the Falkland archipelago.

4.2. Unused biological control agents

Some species have been selected to be used as a biological control agent but have not been used yet: *Ageniosa electoralis* Vogel (Chrysomelinae) was selected to be introduced in Australia to control *Chrysanthemoides monilifera* (Jolivet 2001). *Charidotes pygmaea* Klug (Cassidinae) was selected to be released in Australia to control species of *Lantana* (Jolivet 2001). *Homichloda barkeri* Jacoby (Alticinae) from Kenya was selected to control *Acacia nilotica* in Queensland (Jolivet 2001). *Trachyaphthona sordida* (Baly) (Alticinae) a specialist herbivore on *Paederia foetida* (Skunk Vine) in China and Japan, which is a very invasive weed in Florida spreading in other parts of the Southern Unites States. *Trachyaphthona sordida* is of special interest to be used as a biological agent (Pemberton & Pratt 2002).

Several species have been selected for the control of invasive plants but finally introduction has been abandoned because the species proved to be not selective enough in their food choice. This is the case for example for *Platyphora biforis* (Germar), *P.conviva* (Stål), *P. nigronotata* (Stål) and *P. paraguana* (Jacoby) for the control of Solanaceae (Jolivet 2001).

4.3. The use of indigenous species in biological control

Very rarely indigenous species are successful in controlling nuisance herbs. Both *Chelymorpha cassidea* (F.) (Cassidinae) and *Chirida guttata* (Olivier) (Cassidinae) have been collected in 1979 in Saskatchewan and released in Alberta in an attempt to extend their ranges for the control of *Convolvulus arvensis*, where they did not establish (Julien 1992). In order to control *Calystegia sepium*, native organism of *Chirida guttata* have been collected in Ontario in 1971 and released in British Columbia. They did not establish either (Julien 1992). The same holds true for *Metriona purpurata* native organism collected in 1979 in Saskatchewan and released in Alberta in an attempt to extend its range and control *Convolvulus arvensis* (Julien 1992). However, *Altica foveicollis* Jacoby (Alticinae) a native species of Thailand was used in this country to control *Ludwigia adscendens*. It caused considerable damage with satisfactory degree of control (Julien 1992). *Gastrophysa atrocyanea* a native species introduced in Noto Peninsula (Japan) to control *Rumex obtusifolius* quickly established, increased its population and spread rapidly. Population of the beetle reached satisfactory levels within four years of release (Julien 1992). *Metriona bicolor*, a native organism collected in 1971 in Ontario and released in British Columbia in order to control *Calystegia sepium*, established. In 1985 it was found 14 km from the release site (Julien 1992).

Both *Leptinotarsa defecta* and *L. texana* are indigenous in the USA (Texas) and have been proposed as a biological control agent against three invasive *Solanum* species. The results of the study suggest that of the invasive *Solanum* species, *S. torvum* may be included in the potential host range of *L. texana*. It is suggested that this "new association" approach might result in a substantial control of one of Florida's most invasive solanaceous weeds with acceptable ecological risks (Cuda et al. 2002).

Native biological control agents offer potential advantages over non-native agents, because they may have little impact on non-target native species that have coexisted with the control agent (Sheldon et al. 1995).

4.4. Registered unintentional translocations

Very rarely aspects of unintentional translocations have been registered. In a few cases they can however be reconstructed. Sometimes unintentional introductions have been the result of intentional introduction during a biological control program. *Aphthona nigriscutis* was accidentally released in Canada in 1982 together with *Aphthona cyparissiae*. The release site was treated with herbicide and insecticide in order to eradicate this species (Julien 1992). And *Chrysolina hyperici* is believed to have been introduced accidentally in Hawaii together with *C. quadrigemina* in 1965. It was discovered in 1970 (Julien 1992) and Jolivet (2001) assumes this species is established in Hawaii. In 1979 a *Longitarsus* species referred to as *L. jacobaeae* has been released in Australia from France. This species more closely resembles *L. flavicornis*. It is established and spreading, causing high reduction in weed density at some sites (Julien 1992).

Longitarsus ganglbaueri, a European species, is recently found in Oregon. LeSage (1988) assumed it to be accidentally introduced with those of *L. jacobaeae* imported from Italy and introduced in Oregon.

Xanthogaleruca luteola was accidentally introduced into Britain from Bolzano (Italy) in July 1986. Several specimens had accidentally been transported in camping equipment (SMITH 1990). The single specimen recorded by STERRENBURG (1989) for the Netherlands may also have been based on a displaced specimen. This species has been recorded for the Netherlands only from the very south of the country (BEENEN 1998)

4.5. Non-target effects

Zygogramma bicolorata is an efficient biocontrol agent that can have significant negative impact on the growth and reproduction of *Parthenium hysterophorus* (DHILEEPAN et al. 2000). *Zygogramma bicolorata* breeds in India on small scale on *Xanthium strumarium* and feeds on *Helianthus annuus*. Feeding on *H. annuus* is regarded unwanted non-target feeding. *Parthenium* pollen, which contains parthenin, when deposited on *Helianthus annuus*, makes the latter attractive to beetles in absence of *Parthenium*. Continuous feeding on *Helianthus annuus* retards ovarian development and thus affects fecundity (VIRAKTAMATH et al. 2004).

JULIEN (1992) mentioned the case of *Chrysolina hyperici* that was introduced in New Zealand in 1947 from England to control *Hypericum perforatum* but attacked *Hypericum androsaemum*. Despite some early damage the insect has not persisted on *H. androsaemum* and has not established. In this case the non-target effect did not persist. *Galerucella calmariensis* and *Galerucella pusilla* have been introduced to North America in 1992 as a biological control agent for *Lythrum salicariae* and are now established in many US states and Canadian provinces. At some sites short-term attack on *Rosa multiflora*, *Potentilla anserina* and *Decodon verticillatus* has been observed. This "spillover" does not constitute a host shift since the beetles are unable to complete development on these non-target plants (BLOSSEY et al. 2001).

5. DISCUSSION

It is difficult to give an explanation of the observed relative high number of species from the subfamilies Chrysomelinae, Galerucinae, Alticinae, Cassidinae and Hispinae that have been translocated. It cannot be explained from the representation of these subfamilies within Chrysomelidae. Eumolpinae for example is a large subfamily and is represented in our database by only one species. Although JOLIVET (2001) attributed this to the endogenic life of the larvae of Eumolpinae, this can only be part of the explanation. KIMOTO (1988) showed remarkable differences in the geographical representation of subfamilies in Chrysomelidae. The translocated species originate from all biogeographical regions (Palearctic [47 %], Neotropical [20 %], Nearctic [16 %], Australasian [12 %] and Afrotropical Region [2 %]). The observed representation of subfamilies among the translocated species seems to be a mix of the subfamily representations in these biogeographical regions. For exampled, in the Palearctic Eumolpinae are represented by a low number of species.

It is most likely that the number of unintentional translocations is highly underestimated. Unintentional translocations that did not result in establishment are rarely detected and rarely published. However, unintentional translocations that resulted in establishment and showed negative effects are likely to have been noticed. Such translocations are of importance for our main question, namely the impact of translocations on the biodiversity.

Sometimes the reason why an introduced species has not established is clear. *Altica carduorum* was introduced in Canada in 1963 from Switzerland and France to control *Cirsium arvense*. It did not establish in Alberta, British Colombia, Nova Scotia or Ontario. Slow development in cool summers exposed larvae to high predation (JULIEN 1992). It was also introduced to Great Britain in 1969 and 1970 from France. Several thousands of specimens were released at Silkwood Park, Ascot, Berkshire and at three sites west of Cardiff, Glamorganshire, South Wales (BAKER et al. 1972, COX 2000). They survived the winter in cages only. The climate is too cold and wet to allow survival, except locally (JULIEN 1992). *Chrysolina varians* was introduced in Australia from England in 1930 to control *Hypericum perforatum* and did not establish. It is considered to have suffered from heavy predation and unfavourable climate (JULIEN 1992). It was introduced in Canada from Sweden in 1957 to control *Hypericum perforatum* and did not establish in British Columbia. Release sites were too dry during summer (JULIEN 1992). Adults of the alticinae *Disonycha glabrata* (F.) have been released to control *Amaranthus retroflexus* from Massachusetts (U.S.A.) in Red River Valley, North Dakota in 1979 and 1980 but failed to overwinter (JULIEN 1992). *Longitarsus albineus* was introduced in Australia in 1979 and 1981 from Greece and France to control *Heliotropium europaeum*. Establishment failed due to drought, which eliminated the host (JULIEN 1992). *Physonota alutacea* was introduced in Mauritius from Trinidad in 1947 to control *Cordia curassavica*. It did not establish due to interference by ants (JULIEN 1992).

The observed low percentage of polyphagous species (7 %) that have established after unintentional translocations is not surprising. It seems to be the result of the small proportion of polyphagous Chrysomelidae. Of Chrysomelidae (including Bruchidae) in Central Europe only 19 % are polyphagous, whereas monophagous species contribute 21 % and oligophagous species 60 % (SCHÖLLER 1996).

Although we know of some invasive species that cause a lot of harm, for example *Leptinotarsa decemlineata* and *Diabrotica* species, these species had effect on plants that were non-native culture plants. The spread of the potato over the world was followed by the spread of the insect species associated to it. The same holds for *Diabrotica virgifera* and the increasing culture of corn (*Zea mais*) in Europe. The associated insects will follow the crop when environmental conditions are favourable for the leaf beetle species. *Dicladispa armigera* (Olivier) (Hispinae) was recorded as a pest of rice in Bengal and Bangladesh in 1906. It is the most important hispid pest of rice in tropical Asia, and known from Bangladesh, Myanmar, India, Nepal and China, frequently causing extensive losses of rice crops. Although *D. armigera* is widely distributed throughout India, and frequently causes considerable damage to rice crops, it is only considered as a major pest of rice in Andhra Pradesh, Assam, Bihar, Madhya Pradesh, Manipur, Kerala, Orissa, Indian Punjab, Uttar Pradesh and West Bengal. It is only a rice pest in the southern provinces of China and is present in western Iran and Sumatra, Indonesia and Taiwan (CAB-CPC 2003).

Introduced leaf beetle species affecting native plants seem to be rare. The introduced *Plagiodera versicolora*, *Agelastica alni* and *Xanthogaleruca luteola* are known to damage ornamental trees, and they could cause damage to indigenous woody trees such as *Salix*, *Populus*, *Alnus* or *Ulmus* in North America. However this has never been reported. At present, *Epithrix hirtipennis* native to North and Central America occurs in Italy on several Solanaceae, also on the wild and indigenous species (Maurizio Biondi, L'Aquila-Coppito, pers. comm. 2004) but there is no indication that this causes a threat to biodiversity in Italy.

It seems that negative effects of introduced species on nature are barely recognised. However, this does not mean that they may never occur (DOWNIE 2001). SILFVERBERG (1995) listed the exotic beetle species that have colonized Finland and established themselves outdoors. No leaf beetle was included among the 14 species. This might be due to the climatic conditions in Finland. However, among the more than 200 invasive species listed in the internet invasive species database no Chrysomelidae have been listed (IUCN/SSC 2004). This database focuses on invasive species that are believed to be a threat to biodiversity. From the absence of leaf beetles we might conclude that translocated leaf beetles do not threaten biodiversity yet. This is interesting because there are very alarming situations of leaf beetles attacking cultivated plants (*Diabrotica virgifera*, *Leptinotarsa decemlineata*) or species that have been effectively used as control agent against introduced weeds (*Chrysolina hyperici* and *C. quadrigemina*). In these circumstances, where alien leaf beetle species eradicate a population of a host plant, the host plants grow vigorously because of two different situations: one is the cultivated situation in which the environmental (fertilisation, hydration) and ecological conditions (absence of competition, diseases) favour the host plant very much. A monoculture of good growing plants is the result. The other is a situation in which an alien plant is invading a new environment, mostly in absence of natural enemies or diseases and mostly without competitors. Under more natural conditions the herbivorous beetles find less favourable conditions. When a leaf beetle enters an ecosystem it faces a complex of interrelations in which it first has to establish. It has been shown (KOVALEV 2004) in model studies that this process is more likely to occur in situations where host plants are evenly spread. Under natural conditions this situation rarely occurs. ELTON (2000) promoted in his famous work on ecological invasions, ecological stability to resist invading species.

The threats caused by introduced species on native species are larger than can be concluded from this study on Chrysomelidae. Introduced plant species, introduced carnivorous species, introduced plant or animal diseases, may all have their effect on native leaf beetles. Many cases have been listed in which non-native insects (predators or parasitoids) have been released to control non-native pest species (for examples release of *Oomyzus gallerucae* Fonscolombe (Hymenoptera, Eulophidae) in the United States for the control of *Xanthogaleruca luteola* (PUTTLER & BAILEY 2003). The damage of intentionally introduced species to non-target, native species from these biological controls are rarely documented.

No negative effects on biodiversity of translocated Chrysomelidae have, at present, been reported. The successful control of imported weeds by introduced Chrysomelidae can be seen as a positive effect to biodiversity since some of these weeds prevent natural processes in ecosystems. It is generally accepted that only a minority of alien species become abundant. WILLIAMSON & FITTER (1996) concluded that as many as 80 – 90 % of the established non-indigenous species may actually have minimal detectable effects. Apart from that, introduction of non-indigenous species as a biological control agent is preceded by intensive research to predict the effect of these introductions. BYERS et al. (2002), however, indicated that although there has been a lot of research, we still have little information on the effects on the communities and species we are attempting to protect. They propose key research questions to effectively prioritise and manage non-indigenous species.

Although there are no cases known in which biodiversity is threatened by translocated Chrysomelidae this is no guarantee that it will not happen. Accidental translocations must be avoided as much as possible. No intentional translocations should be considered until the factors, which limit its distribution and abundance in its native range, have been understood. The approach suggested by the IUCN (1987, 2000) will minimise the risks.

The Convention on Biological Diversity (Rio de Janeiro 1992) called for prevention of the introduction of, control or eradication of those alien species, which threaten ecosystems, habitats or species. However it proved to be difficult to discriminate between alien species that are likely to be invasive and those that are not. Because post entry control of invasive alien species is much more costly than prevention of invasions, MACK et al. (2000) suggested that national and international quarantine laws should be altered by adopting a "guilty until proven innocent" approach.

A rarely studied risk of alien species is the role of evolutionary processes. KOVALEV (2002) showed changes in the introduced *Zygogramma suturalis* which developed flight ability and morphological differences within five generations. The differences where large enough to attribute the Palearctic population to a new subspecies: *Z. suturalis volutes* KOVALEV. About the risk of hybridisation between native leaf beetle species and alien species nothing is clear. Hybridisations between native and alien plants species or between genetically different populations of alien plants are believed to promote rapid evolution and further invasion as has been observed in *Spartina anglica* (polyploid hybrid of *S. alterniflora* from eastern America and the European *S. maritima*) and *Rhododendron ponticum* (introduced from several different Iberian populations) (PETIT 2004).

Apart from natural processes as the post glacial spread of many species (including spread across barriers as the Alps and Pyrenees in Europe), human-induced translocations may have started as soon as man appeared.

In Europe the invasion of alien species started in ancient times. The original landscape most probably was a mosaic of forest and open areas. When man arrived large areas were cleared for agriculture. Plant and animal species from deserts and steppes invaded the European region when new, cultivated, habitats appeared. Already at the time of Columbus the coastland of Western Europe was almost devoid of forests and transformed into an artificial steppe inhabited by man's constant followers among plants and animals, invited or self-invited (LINDROTH 1957). Part of theses species have simply expanded their range but it is very likely that part of them were actively transported with seeds or with the transport of livestock (both plants and animals). It is very likely that leaf beetle species associated with crops or the herbs that grow between them have taken the same route as herbs associated with cereals. They are supposed to have arrived in Europe from the Near East (PINHASI *et al.* 2005). This process is still going on. HAMMOND (1974) assumed that some of the relative recent immigrants to the British Isles may represent delayed movements of the same kind. An example of such a species combination may be *Buglossoides* (= *Lithospermum*) *arvensis* and *Longitarsus fuscoaeneaus* REDTENBACHER. Both species are nowadays indigenous in Europe. It is believed that *B. arvensis* originated in southwest-Asia and spreaded with agriculture to large parts of the temperate parts of the Northern Hemisphere. In The Netherlands it already occurred during the Roman times (WEEDA *et al.* 1988). It is likely that *L. fuscoaeneus* spreaded with this herb. FRITZ-KÖHLER (1996) and FRITZLAR (1998) estimate that about 5% of the leaf beetles of the German states Rhineland and Thüringia came along with introduced plants (neophytes and archeophytes).

In America conditions were different when transatlantic trade started. In northeastern North America the tribes were more or less migratory and had hardly progressed beyond the Neolithic stage. Therefore in North America, the chance of native steppe plants invading permanent arable land and transforming into constant weeds was considerably less than in the old world. When the first Europeans arrived and permanent settlements were founded upon which agriculture started, there were few indigenous plants present able to intrude as weeds. This gave free entrance to the corresponding floral elements from Europe. Species introduced from Europe into North America are about ten times as numerous as those transported in the opposite direction (LINDROTH 1957). This is partly explained by the peculiar character of ballast traffic in the 19th century. The small sailing vessels used for commercial traffic needed cargo or ballast to be sailed efficiently. On their way to Northern American ports they often were short in tonnage. The bottom of the lower holds were then filled with material available at the shore of departure: gravel, rocks or even moist sand. On arrival at their destination the ballast was dumped on the coast, including the plants and animals that came along with this material. Examples of leaf beetles that have been transported in this way are *Cassida flaveola*, *Chrysolina staphylea* and *Gastrophysa polygoni* (LINDROTH 1957).

Not all translocations have to be human-induced. CLARKE & ZALUCKI (2004) suggested, based on historical information, that a substantial population of the monarch butterfly (*Danaus plexippus* (L.), Danaidae) was carried to Australia on winds associated with cyclones that hit the Queensland coast in early 1870. The leaf beetle *Chaetocnema confinis*, originally a North American species, has spread to tropical America, Africa, Asia and the Pacific, accidentally introduced in Hawaii and established, it is reported to be transported by a hurricane (JOLIVET 2001). *Stegnaspa trimeni* is common on Tristan da Cunha and originated from Southern Africa, most probably it was accidentally introduced or transported eolic (hurricane ?) (JOLIVET 1998). *Epithrix hirtipennis* from North and Central America was recorded in 1984 from the Azores and Italy (DÖBERL 1994a). Subsequently it spreaded to Greece (1988) and Turkey (1993). Although introduction with cultivated plants is possible, spreading with passatwinds is also suggested as a possibility (DÖBERL 1994a).

Acknowledgments. S. M. Clark, M. Biondi, D. Erber (†) and M. A. Hielkema kindly supported this study either be supplying information or supplying specimens from which conclusions were drawn. Theresa Canning (CAB International) kindly offered a free trial of the internet version of the Crop Protection Compendium. P. Jolivet stimulated this study by many references to useful publications. D. G. Furth, T. Wagner and an anonymous reviewer made valuable comments on a previous version of this article. Participating in the 6th International Symposium on the Chrysomelidae was possible with a grant from the "Uyttenboogaart-Eliasen Stichting tot bevordering van de entomologische wetenschap".

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Appendix 1

Table of translocated leaf beetle species with information on the translocation events, the success of the translocation and the host plants. For all records the information source is presented. Status: E = established; N = not established; D = doubtful. Intention: I= intentional; U = unintentional. Subfamily abbreviations: CRIO = Criocerinae; ZEUG = Zeugophorinae; CRYP = Cryptocephalinae; EUMO = Eumolpinae; CHLA = Chlamisinae; CHRY = Chrysomelinae; GALE = Galerucinae; ALTI = Alticinae; CASS = Cassidinae; HISP = Hispinae.

Species	Subfamily	Indigenous	Destination	Status	Date	Host	Reference	Intention
Acalymma vittatum (Fabricius)	ALTI	Central USA	West USA	E	?	Cucumber	CAB-CPC 2003	U
Agasicles hygrophila Selman & Vogt	ALTI	Argentina	USA	E	1964	*Alternanthera philoxeroides*	Julien 1992; Hawkes et al. 1967	I
			Australia	E	1977		Julien 1992	I
			New Zealand	E	1981		Julien 1992	I
			Thailand	E	1982		Julien 1992	I
			P. R. China	?	1986		Julien 1992	I
Agelastica alni (Linnaeus)	GALE	Europe	Northeast USA	E	?	*Alnus glutinosa*	Lindroth 1957	U
Alagoasa parana Samuelson	ALTI	Brazil	Australia	N	1981	*Lantana camara*	Julien 1992	I
			Rep. South Africa	N	1985		Julien 1992	I
Altica carduorum Guérin-Méneville	ALTI	Continental Europe	Canada	N	1963	*Cirsium arvense*	Julien 1992	I
			Great Britain	N	1969, 1970		Julien 1992	I
			New Zealand	?	1999		Julien 1992	I
			USA	N	1966, 1970			I
		P. R. China	USA	?	?		Jolivet 2001	I
Altica foveicollis Jacoby	ALTI	Thailand	Thailand	E	?	*Ludwigia adscendens*	Julien 1992	I
Anacassis fuscata (Klug)	CASS	Australia	Brazil	N	1976	*Baccharis halimifolia*	Julien 1992	I
Anacassis phaeopoda Buzzi	CASS	Australia	Brazil	N	1976	*Baccharis halimifolia*	Julien 1992	I
Aphthona abdominalis (Duftschmid)	ALTI	Europe	USA	E	1993	*Euphorbia esula*	Jolivet 2001; Schroeder & Gassmann 1997	I
Aphthona cyparissiae (Koch)	ALTI	Europe	Canada	E	1982	*Euphorbia cyparissias*	Julien 1992	I
				E	1982	*Euphorbia x pseudovirgata, E. esula*	Julien 1992; Schroeder & Gassmann 1997	I

Aphthona cyparissiae (Koch)			USA		1986	*Euphorbia x pseudovirgata, E. esula*	JULIEN 1992; SCHROEDER & GASSMANN 1997	I
Aphthona czwalinai (Weise)	ALTI	Europe	Canada	N	1987	*Euphorbia cyparissias*	JULIEN 1992	I
			Canada	E	1985, 1989, 1990	*Euphorbia x pseudovirgata, E. esula*	JULIEN 1992; SCHROEDER & GASSMANN 1997	I
			USA	E	1987	*Euphorbia x pseudovirgata, E. esula*	JULIEN 1992; SCHROEDER & GASSMANN 1997	I
Aphthona flava Guillebeau	ALTI	Europe	Canada	N	1982	*Euphorbia cyparissias*	JULIEN 1992	I
				E	1982	*Euphorbia x pseudovirgata, E. esula*	JULIEN 1992; SCHROEDER & GASSMANN 1997	I
			USA	E	1985	*Euphorbia x pseudovirgata, E. esula*	JULIEN 1992; SCHROEDER & GASSMANN 1997	I
			Canada	E	1990	*Euphorbia esula*	SCHROEDER & GASSMANN 1997	I
			USA	E	1993	*Euphorbia esula*	SCHROEDER & GASSMANN 1997	I
Aphthona nigriscutis Foudras	ALTI	Europe	Canada	N	1982	*Euphorbia cyparissias*	JULIEN 1992	U
				E	1983	*Euphorbia esula, E. cyparissias,*	JULIEN 1992; SCHROEDER & GASSMANN 1997	I
				N	1982	*Euphorbia x pseudovirgata*	JULIEN 1992	U
				E	1983		JULIEN 1992; SCHROEDER & GASSMANN 1997	I
			USA	E	1989	*Euphorbia x pseudovirgata*	JULIEN 1992; SCHROEDER & GASSMANN 1997	I
Argopistes gourvesi Samuelson	ALTI	Tahiti	Archipel de Tahiti	E	?	Oleaceae	JOLIVET 2001	U
Aspidimorpha deusta (Fabricius)	CASS	Asia: East of Java	Malaysia	E	?	*Ipomoea pes-caprae*	VELU 2001	U

Species	Subfamily	Indigenous	Destination	Status	Date	Host	Reference	Intention
Aspidimorpha nigropunctata (Klug)	CASS	Africa	Netherlands	N	1988	?	Beenen, unpubl.	U
Aulacophora indica (Gmelin)	GALE	Asia, Oceania	Canada: Vancouver	N	1964	Cucurbitaceae	Beenen, unpubl.	U
Brontispa chalybeipennis (Zacher)	HISP	?	Hawaii.	E	?	Palms	Jolivet 2001	U
Brontispa longissima Gestro	HISP	Indonesia, Papua New Guinea, Irian Jaya.	Japan: Okinawa	E	1978	Palms	Morimoto & Kiritani 1995	U
Calligrapha pantherina Stål	CHRY	Mexico	Australia	E	1989	*Sida acuta*	Julien 1992	I
				E	1989	*Sida rhombifolia*	Julien 1992	I
Calligrapha polyspila (Germar)	CHRY	Nearctic	Azores	E	?	*Sida rhombifolia*	Jolivet 2001	U
Cassida azurea Fabricius	CASS	Europe	Canada	?E	1989	*Silene vulgaris*	Julien 1992	I
			USA	E	?		Jolivet 2001	I
Cassida circumdata Herbst	CASS	Indomalaysia	Hawaii	E	?	Convolvulaceae	Jolivet 2001	U
Cassida flaveola Thunberg	CASS	Europe	Eastern USA, Canada	E	?	Cariophyllaceae	Lindroth 1957	U
Cassida miliaris Fabricius	CASS	Southeast Asia	St. Helena	N	?	*Ipomoea*, *Convolvulus*	Jolivet 2001	U
Cassida obtusata Boheman	CASS	Southeast Asia	Japan	E	?	Amaranthaceae	Morimoto & Kiritani 1995	U
Cassida rubiginosa Müller	CASS	Europe	Canada	E	prior 1902	*Carduus acanthoides*, *Carduus nutans*	Julien 1992	U
			USA	E	±1901	*Carduus rthoermeri*, *Cirsium vulgare*	Spring & Kok 1999 Lindroth 1957	U
Chaetocnema concinna (Marsham)	ALTI	Europe	Canada, USA	E	?	*Polygonum persicariae*, *Sorghum sudanense*	LeSage 1990 Lindroth 1957	U
Chaetocnema confinis Crotch	ALTI	USA	tropical America, Africa, Asia and the Pacific	E	?	*Ipomoea*	Jolivet 1998 Jolivet 2001	U
Chlamisus mimosae Karren	CHLA	Brazil	Australia	E	1985	*Mimosa pigra*	Julien 1992	I
			Thailand	E	1986		Julien 1992	I
			Vietnam	?	1999		Julien 1992	I

Chlamisus gibbosa (Fabricius)	CHLA	U.S.A (Missouri)	Hawaii	N	1969	*Rubus argutus*	JULIEN 1992	I
Chrysolina bankii (Fabricius)	CHRY	Europe	Azores	E	?	Labiatae	JOLIVET 2001	U
Chrysolina brunsvicensis (Gravenhorst)	CHRY	England	Australia	N	1930	*Hypericum perforatum*	JULIEN 1992	I
Chrysolina gypsophilae Küster	CHRY		USA	E	?	*Linaria genistifolia dalmatica*	JOLIVET 2001	I
Chrysolina hyperici (Forster)	CHRY	England	New Zealand	E	1943	*Hypericum perforatum*	JULIEN 1992; FIELDS et al. 1988	I
			Australia	E	1930		JULIEN 1992	I
		France	Australia	?	1980		JULIEN 1992	I
		England via Australia via U.S.A	Canada	E	1951		JULIEN 1992; FIELDS et al. 1988	I
		England via Australia	USA	E	1945		JULIEN 1992; FIELDS et al. 1988	I
		England via Australia via USA	Chile	E	1953		JULIEN 1992	I
		England via Australia	Rep. South Africa	N	1960		JULIEN 1992	I
		England via Australia via USA via Canada		D	1973		JULIEN 1992	I
			Hawaii	E	1965		JULIEN 1992; JOLIVET 2001	U
Chrysolina polita (Linnaeus)	CHRY		Lesser Antilles	N	?		JOLIVET 2001	U
Chrysolina quadrigemena (Suffrian)	CHRY	France	Australia	E	1939	*Hypericum perforatum*	JULIEN 1992; FIELDS et al. 1988	I
		France via Australia via USA	Canada	E	1952		JULIEN 1992; FIELDS et al. 1988	I
		France via Australia via USA	Chile	E	1953		JULIEN 1992	I
		France via Australia via California	Hawaii	E	1965		JULIEN 1992	I
		France via Australia	New Zealand	E	1963		JULIEN 1992; FRASER & EMBERSON 1987	I
		France via Australia	South Africa	E	1961		JULIEN 1992	I
		France via Australia	USA	E	1946		JULIEN 1992; FIELDS et al. 1988	I

Species	Subfamily	Indigenous	Destination	Status	Date	Host	Reference	Intention
Chrysolina staphylea (Linnaeus)	CHRY	Palearctic	Nova Scotia (Canada)	E	?	*Plantago*	LINDROTH 1957	U
Chrysolina varians (Schaller)	CHRY	England	Australia	N	1930	*Hypericum perforatum*	JULIEN 1992	I
		Sweden	Canada	N	1957			I
		Europe	USA	N	1950		JULIEN 1992	I
Colposcelis signata (Motschulsky)	EUMO	Southeast Asia	Hawaii	E	?	Fabaceae	JOLIVET 2001	U
Crioceris asparagi (Linnaeus)	CRIO		Eastern USA	E		*Asparagus officinalis*	LINDROTH 1957	U
Crioceris decempunctata Linnaeus	CRIO		Eastern USA	E		*Asparagus officinalis*	LINDROTH 1957	U
Diabrotica undecimpunctata Mannerheim	GALE	USA	Hawaii	N	?		JOLIVET 2001	U
Diabrotica virgifera virgifera LeConte	GALE	Central America	North America	E	after 1000	*Zea mais*	GRAY & STEFFEY 1999	U
			Europe	E	1992		GRAY & STEFFEY 1999	U
Diachus auratus (Fabricius)	CRYP	Central America	New Caledonia, Australia, Pacific Region (Hawaii, Tahiti)	E	?	Polyphagous	JOLIVET 2001	U
Diorhabda elongate Brullé	GALE		USA	E	?	*Tamarix ramosissima*	JOLIVET 2001	I
Disonycha argentinensis Jacoby	ALTI	Brazil	Australia	N	1980	*Alternanthera philoxeroides*	JULIEN 1992	I
			New Zealand	N	1982		JULIEN 1992	I
Disonycha glabrata (Fabricius)	ALTI	MS (U.S.A.)	ND (U.S.A.)	N	1979/80	*Amaranthus retroflexus*	JULIEN 1992	I
Epithrix fasciata Blatchely	ALTI	Brazil	Hawaii	E	?	Solanaceae	JOLIVET 2001	U
Epithrix hirtipennis (Melsheimer)	ALTI	North and Central America	Azores and	E	1984	Solanaceae	DÖBERL 1994a	U
			Italy	E	1984		DÖBERL 1994a; SANNINO et al. 1985	U

Epithrix hirtipennis (Melsheimer)			Greece	E	1988		Döberl 1994a	U
			Turkey	E	1993		Döberl 1994a	U
			Hawaii	E	?		Jolivet 2001	U
Galeruca rufa Germar	GALE	Europe	USA	E	?	*Convolvuls arvensis, C. sepium*	Jolivet 2001	I
Galerucella calmariensis (Linnaeus)	GALE	Germany	USA	E	1992	*Lythrum salicariae*	Hight et al. 1995	I
			Canada	E	1992		Hight et al. 1995	I
Galerucella pusilla (Duftschmid)	GALE	Germany	USA	E	1992	*Lythrum salicariae*	Hight et al. 1995	I
			Canada	E	1992		Hight et al. 1995	I
Gastrophysa atrocyanea Motschulsky	CHRY	Japan	Noto Peninsula (Japan)	E	?	*Rumex obtusifolius*	Julien 1992	I
Gastrophysa polygoni (Linnaeus)	CHRY	Palearctic	USA, Canada	E	?	Polygonaceae	Lindroth 1957	U
Lema bilineata (Germar)	CRIO	Argentina	South Africa	E	± 1900	Solanaceaea	Jolivet 2001	U
Lema cyanella (Linnaeus)	CRIO	Switzerland	Canada	N	1978/83	*Cirsium arvense*	Julien 1992	I
			New Zealand	N	1983/90		Julien 1992	I
			USA	N	?		Jolivet 2001	I
Lema trilinea White	CRIO	Northern America	Hawaii	E	?	Solanaceae	Jolivet 2001	U
			South Africa	E	± 1900	Solanaceaea	Jolivet 2001	U
Leptinotarsa decemlineata Say	CHRY	Rocky Mountains	USA, Canada,	E	1859	Solanaceaea	Lindroth 1957	U
			Europe	E	1922			
			Lesser Antilles	N	?		Jolivet 2001	U
Leptinotarsa defecta (Stål)	CHRY	USA	South Africa	E	1992	*Solanum elaeagnifolium*	Hoffmann et al. 1998, Cuda et al. 2002	I
Leptinotarsa texana (Schaeffer)	CHRY	USA	South Africa	E	1992	*Solanum elaeagnifolium*	Hoffmann et al. 1998, Cuda et al. 2002	I
Lilioceris lilii Scopoli	CRIO	Palearctic	Montreal (Canada)	E	1945	Liliaceae	Lindroth 1957	U
			USA	E	1992		University of Rhode Island 2002	U
Lioplacis elliptica (Stål)	CHRY	Brazil	Australia	N	1977	*Baccharis halimifolia*	Julien 1992	I

Species	Subfamily	Indigenous	Destination	Status	Date	Host	Reference	Intention
Longitarsus aeneus Kutschera	ALTI	Mediterranean	Australia	?	?	*Echium plantagineum*	Jolivet 2001	I
Longitarsus albineus (Foudras)	ALTI	Greece and France	Australia	N	1979, 1981	*Heliotropium europaeum*	Julien 1992	I
Longitarsus echii (Koch)	ALTI	Palearctic	Australia	?	?	*Echium plantagineum*	Jolivet 2001	I
Longitarsus ferrugineus (Foudras)	ALTI	Europe	USA, Canada	E	?	*Mentha*	Lindroth 1957; LeSage 1988	U
Longitarsus flavicornis (Stephens)	ALTI	Spain	Australia	E	1985	*Senecio jacobaea*	Julien 1992	I
		Britain	Canada	E	1971	*Senecio jacobaea*	Julien 1992	I
Longitarsus ganglbaueri Heikertinger	ALTI	? Italy	Oregon (USA)	E		*Senecio*	LeSage 1988	U
Longitarsus jacobaeae (Waterhouse)	ALTI	Italy	USA	E	1969	*Senecio jacobaea*	Julien 1992; LeSage 1988	I
		Italy via USA	Canada	E	1971		Julien 1992; LeSage 1988	I
		Italy via USA	New Zealand	E	1983		Julien 1992	I
		Italy via USA via New Zealand	Australia	E	1988		Julien 1992	I
Longitarsus luridus (Scopoli)	ALTI	Europe	USA, Canada	E	?	Plantaginaceae	LeSage 1988	U
Longitarsus pellucidus (Foudras)	ALTI	Europe	Ontario (Canada)	?	?	Convolvulaceae	LeSage 1988	U
Longitarsus pratensis (Panzer)	ALTI	Europe	USA, Canada	E	?	Plantaginaceae	LeSage 1988; Jolivet 2001	U
Longitarsus rubiginosus (Foudras)	ALTI	Europe	Canada (Québec, Ontario)	E	?	Convolvulaceae	LeSage 1988	U
Longitarsus succineus (Foudras)	ALTI	Europe	Newfoundland (Canada)	E	?	Asteraceae	Lindroth 1957; LeSage 1988	U
Macrima pallida (Laboissière)	GALE	Himalaya range	Cyprus	?	?		Beenen unpubl.	U
Mantura chrysanthemi Koch	ALTI	Europe	USA (Massachusetts)	?	?	Poylgonaceae	Lindroth 1957; Jolivet 2001	U
Metallactus nigrofasciatus Suffrian	CRYP	Brazil	Australia	N	1982	*Baccharis halimifolia*	Julien 1992	I

Metallactus patagonicus Suffrian	CRYP	Brazil	Australia	N	1974	*Baccharis halimifolia*	JULIEN 1992	I
Metriona bicolor (Fabricius)	CASS	Ontario (Canada)	British Columbia (Canada)	E	1971	*Calystegia sepium*	JULIEN 1992	I
Metriona purpurata (Boheman)	CASS	Saskatchewan (Canada)	Alberta (Canada)	N	1979	*Convolvulus arvensis*	JULIEN 1992	I
Metrogaleruca obscura (Degeer)	GALE	Trinidad	Malaysia	?	1977 ?	*Cordia curassavica*	JULIEN 1992	I
			Mauritius	E	1948		JULIEN 1992	I
		Trinidad via Malaysia	Sri Lanka	E	1948		JULIEN 1992	I
Microtheca ochroloma Stål	CHRY	Argentina and Uruguay	USA	E	?	Brassicaceaea	JOLIVET 2001	U
Microtheca picea (Guérin)	CHRY	Argentina and Uruguay	USA	E	?	Brassicaceae	JOLIVET 2001	U
Monoxia minuta Blake	GALE	USA	Hawaii	E	?	*Chrysothamnus*	JOLIVET 2001	U
Neolochmaea dilatipennis (Jacoby)	GALE	Panama	Miami (USA)	E	?	*Borreria terminalis*	JOLIVET 2001; JOLIVET & HAWKESWOOD 1995	U
Octacoma championi Baly	HISP	Costa Rica	Australia	E	1975	*Lantana camara*	JULIEN 1992	I
			Norfolk island	?	1988		JULIEN 1992	I
		Central America via Australia	Fiji	N	1976		JULIEN 1992	I
		Central America via Australia	South Africa	N	1978		JULIEN 1992	I
Octacoma plicatula (Fabricius)	HISP	?	Hawaii	N	1954	*Lantana camara*	JULIEN 1992	I
Octocoma scabripennis Guérin-Méneville	HISP	Mexico via Hawaii	Australia	E	1966	*Lantana camara*	JULIEN 1992; JOLIVET & HAWKESWOOD 1995	I
			Norfolk island	E	1971		JULIEN 1992	I
		El Salvador	Australia	E	1974		JULIEN 1992; JOLIVET & HAWKESWOOD 1995	I
		Mexico via Hawaii via Australia	Cook Islands	N	1973		JULIEN 1992	I
		Mexico via Australia	Fiji	N	1971, 1976		JULIEN 1992	I
		Mexico via Hawaii via Australia	Ghana	E	1971, 1973		JULIEN 1992; JOLIVET & HAWKESWOOD 1995	I
		Mexico	Hawaii	N	1902		JULIEN 1992	I

Species	Subfamily	Indigenous	Destination	Status	Date	Host	Reference	Intention
Octocoma scabripennis Guérin-Méneville		Mexico	Hawaii	E	1954		Julien 1992	I
		Mexico via Hawaii via Australia	India	E	1921		Julien 1992	I
		from Mexico via Hawaii	Mariana Islands	N	1971		Julien 1992	I
		Mexico via Hawaii via Australia	New Caledonia	E	1977		Julien 1992	I
		Mexico via Hawaii via Australia	South Africa	E	1971, 1974		Julien 1992; Jolivet & Hawkeswood 1995	I
Ophraella communa LeSage	GALE	North America	Honshu (Japan)	E	1996	*Ambrosia artemisiifolia, A. trifida*	Suzuki & Nakamura 1999; Watanabe & Hirai 2004	U
			Taiwan	E	1996		Wang & Chiang 1998	U
			China	E	2004		Zhang et al. 2005	U
Oulema melanopus (Linnaeus)	CRIO	Palearctic	USA	E	?	Gramineae	Jolivet 2001	U
Paropsis charybdis Stål	CHRY	Australia	South Africa	E	?	*Eucalyptus*	Jolivet 2001	U
			New Zealand	E	?		Jolivet 2001	U
Pentispa suturalis Baly	HISP	?	USA	E	?	*Baccharis bigelovii*	Jolivet 2001	I
Phaedon armoraciae L. (identification needs confirmation !)	CHRY	Palearctic	Canada	E	?	*Veronica beccabunga*	Lindroth 1957	U
Phaedon cochleariae Fabricius (identification needs confirmation !)	CHRY	Palearctic	USA, Canada	E	?	Brassicaceae	Lindroth 1957	U
Phyllocharis undulata (Linnaeus)	CHRY	Vietnam	Thailand	E	1990	*Clerodendrum philippinum*	Julien 1992	I
Phyllotreta aerea Allard	ALTI	Palearctic	Northeast USA	E	?	Brassicaceae	Lindroth 1957	U
Phyllotreta armoraciae Koch	ALTI	Palearctic	Northeast USA, Eastern Canada	E	?	*Armoracia rusticana*	Lindroth 1957; Dillon & Dillon 1972	U
Phyllotreta cruciferae (Goeze)	ALTI	Eurasian	North America	E	± 1920	Cruciferae (crops)	CAB-CPC	U

Phyllotreta undulata Kutschera	ALTI	Palearctic	Maryland	E	?	Brassicaceae	Lindroth 1957	U
Phyllotreta vittata Fabricius	ALTI	Palearctic	North America	E	?	Brassicaceae	CAB-CPC 2003	U
			South Africa	E	?		CAB-CPC 2003	U
Physonota alutacea Boheman	CASS	Trinidad	Mauritius	N	1947	*Cordia curassavica*	Julien 1992	I
Plagiodera versicolora Laicharting	CHRY	Palearctic	Northeastern USA, Eastern Canada	E	1911	*Salix* and *Populus*	Lindroth 1957; Elton 2000; Jolivet 2001	U
Promecotheca papuana Csiki	HISP		Queensland (Australia)	D	?	Coconut	CAB-CPC 2003	U
Pseudolampsis guttata (LeConte)	ALTI	Argentina and Uruguay	USA	E	?	*Azolla*	Jolivet 2001; Jolivet & Hawkeswood 1995	U
Pseudorupilia ruficollis (Fabricius)	GALE	South African	Sainte Hélène	N	?	Restionaceae, Proteaceae, Asteraceae	Jolivet 2001	U
Psylliodes chalcomerus (Illiger)	ALTI		USA	E	?	*Carduus nutans*	Jolivet 2001	I
Psylliodes chrysocephalus Linnaeus	ALTI		Newfoundland (Canada)	E	?	Brassicaceae	Lindroth 1957	U
Psylliodes cucullatus Illiger	ALTI	Palearctic	Eastern Canada	E	?	?	Lindroth 1957	U
Psylliodes picina (Marsham)	ALTI		USA	E	?	*Lythrum*, *Lysimachia*	Lindroth 1957	U
Silana farinosa (Boheman)	CASS	Sri Lanka	Malaysia	E	?	Curry leaves	Velu 2001	U
Stegnaspa trimeni Baly	ALTI	Southern Africa	Tristan da Cunha	E	?	?	Jolivet 2001	U
Stolas fuscata (Klug)	CASS	Argentina	USA	E	?	*Baccharis salicifolia*	Jolivet 2001	I
Stolas ingrata (Boheman)	CASS	Argentina	USA	E	?	*Gutierrezia* spp.	Jolivet 2001	I
Systena blanda Melsheimer	ALTI	USA	Hawaii	E	?	polyphagous	Jolivet 2001	U
Timarcha goettingensis-complex	CHRY	Europe	Gran Canaria (Islas Canarias)	N	?	*Galium*	Jolivet & Verma 2002	U
Trachymela tincticollis (Blackburn)	CHRY	Australia	South Africa	E	?	*Eucalyptus*	Jolivet 2001	U
Trirhabda baccharidis (Weber)	GALE	USA	Australia	E	1969	*Baccharis halimifolia*	Julien 1992	I

Species	Subfamily	Indigenous	Destination	Status	Date	Host	Reference	Intention
Uroplata girardi Pic	HISP	Brazil via Hawaii	Australia	E	1966	*Lantana camara*	JULIEN 1992; JOLIVET & HAWKESWOOD 1995	I
			Norfolk Island	E	1971		JULIEN 1992	I
		Brazil via Hawaii	Caroline Islands	E	1963, 1974		JULIEN 1992	I
		Brazil via Hawaii via Australia via Fiji	Cook Island	E	1969		JULIEN 1992	I
		Brazil via Hawaii via Australia via India	Cook Island	E	1976		JULIEN 1992	I
		Brazil via Hawaii	Fiji	E	1969		JULIEN 1992	I
		Brazil via Hawaii	Ghana	E	1971		JULIEN 1992; JOLIVET & HAWKESWOOD 1995	I
		Brazil	Hawaii	E	1961		JULIEN 1992	I
		Brazil via Hawaii	India	E	1972		JULIEN 1992	I
		Brazil via Hawaii	Mariana Islands	E	1963/1967		JULIEN 1992	I
		Trinidad	Mauritius	E	1967		JULIEN 1992	I
		Brazil via Hawaii via Australia	New Caledonia	E	1977		JULIEN 1992	I
		Brazil via Hawaii via Australia	Papua New Guinea	E	1972		JULIEN 1992	I
		Brazil via Hawaii via Fiji	Philippines	E	1985		JULIEN 1992; BEENEN, unpubl.	I
		Argentina, Brazil, Paraguay via Hawaii via Australia	South Africa	E	1974, 1981		JULIEN 1992; JOLIVET & HAWKESWOOD 1995	I
		Trinidad via Mauritius	South Africa	E	1984		JULIEN 1992; JOLIVET & HAWKESWOOD 1995	I
		Brazil via Trinidad	Tanzania	N	1967		JULIEN 1992	I
		Brazil via Hawaii via Australia via Fiji	Tonga Islands	E	1969		JULIEN 1992	I
Uroplata lantanae Buzzi & Winder	HISP	Brazil	Australia	N	1977	*Lantana camara*	JULIEN 1992	I
		Brazil via Australia	South Africa	N	1984		JULIEN 1992	I
Uroplata sp. near *bilineata* Chapuis	HISP	Brazil	Australia	E	1976	*Lantana camara*	JULIEN 1992	I
		Central America	Fiji	N	1976	*Lantana camara*	JULIEN 1992	I

Uroplata sp. near *bilineata* Chapuis		Costa Rica via Australia	South Africa	N	1978	*Lantana camara*	Julien 1992	I
Xanthogaleruca luteola (Müller)	GALE	Europe	North America	E	± 1834	*Ulmus*	Clark pers. comm.; Krafsur & Nariboli 1995	U
		?	Morocco	E	?		Jolivet 1967	U
		Bolzano (Italy)	Britain	?	1986		Smith 1990	U
			Australia	E	1980		Jolivet 2001	U
Zeugophora scutellaris Suffrian (Identification needs confirmation !	ZEUG	Palearctic	USA	E	?	*Populus nigra*	Lindroth 1957	U
Zygogramma bicolorata Pallister	CHRY	Mexico	Australia	E	1980	*Parthenium hysterophorus*	Julien 1992; Dhileepan et al. 2000	I
		Mexico	India	E	1984		Julien 1992; Dhileepan et al. 2000	I
Zygogramma disrupta Rogers	CHRY	USA	the North Caucasus	?	1990	*Ambrosia artemisiifolia*	Julien 1992	I
Zygogramma suturalis Fabricius	CHRY	USA and Canada	Peoples Republic of China	?	1978	*Ambrosia artemisiifolia*	Julien 1992	I
		USA and Canada	Union of Soviet Republics	E	1978		Julien 1992	I
		Canada	Union of Soviet Republics	E	1979	*Ambrosia maritima.*	Julien 1992	I
		USA and Canada	Australia	?	1990		Julien 1992	I
		USA and Union of Soviet Republics	Yugoslavia	?	?		Julien 1992	I

Bonner zoologische Beiträge	Band 54 (2005)	Heft 4	Seiten 201–208	Bonn, Oktober 2006

Functional Morphology of Copulation in Chrysomelidae-Criocerinae and Bruchidae (Insecta: Coleoptera)[1]

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Abstract. Until now, the genitalia of beetles have been investigated mainly under taxonomic aspects while there exist few studies on the functional morphology of genital structures. Many questions concerning the position of male genitalia inside the female during copulation, the functional role of parameres and endophallus, the mechanical coupling of the mates as well as sperm transfer remain unsolved for most species of Coleoptera. This article presents results gained from investigations of pairs of *Acanthoscelides obtectus* (Bruchidae), *Oulema melanopus, Oulema duftschmidi* and *Lilioceris lilii* (Criocerinae) fixed in copula. During copulation parameres remain outside the female in *Acanthoscelides.* In Criocerinae, the flagellum is placed near the entrance of the spermathecal duct. Campaniform sensilla were found on the surface of the endophallus in *Lilioceris.*

Key words. endophallus, flagellum, aedeagus, sperm-transfer, parameres, bursa copulatrix, *Acanthoscelides obtectus, Lilioceris lilii, Oulema duftschmidi, Oulema melanopus*

1. INTRODUCTION

Most evolutionary variations can be interpreted as a means to increase fitness. Anything connected with reproduction is of central importance for this increase. The functional morphology of copulation, however, is unknown for most species of beetles. There exist studies on the functional morphology of genitalia in insects in general (HEBERDEY 1928, 1931) and in several beetle species. NYHOLM (1969) for example, analysed the structure and function of the copulatory organs of *Cyphon* species (Coleoptera: Scirtidae). EBERHARD (1993) studied courtship and genital mechanics of three species of *Macrodactylus* (Coleoptera: Scarabaeidae). Spermathecal morphology and sperm transfer of the staphylinid beetle, *Aleochara curtula* (Coleoptera: Staphylinidae), are well understood (GACK & PESCHKE 1994; FÖRSTER et al. 1998). HAUBRUGE et al. 1999 found that in *Tribolium castaneum* (Coleoptera: Tenebrionidae) the male removes the sperm of previous males from the female tract by means of its median lobe. In *Cicindela* (Coleoptera: Cicindelidae) as well, the males seem to clear the spermatheca and the spermathecal duct with its flagellum before they place the spermatophore (FREITAG et al. 2001). Since all these groups are not closely related to the Chrysomelidae, the results may not be applicable to our group.

One of the first studies on the functional morphology of genitalia in Chrysomelidae is that of HARNISCH (1915) who described the copulatory apparatus of *Chrysomela populi*, *Clytra quadripunctata* and *Plateumaris sericea.* RODRIGUEZ et al. (2004) found that females of *Chelymorpha alternans* (Chrysomelidae: Cassidinae) prefer males with a longer flagellum. This result confirms the cryptic female choice hypothesis (THORNHILL 1983; EBERHARD 1985, 1997). CRUDGINGTON & SIVA JOTHY (2000) observed that the males of *Callosobruchus maculatus* (Coleoptera: Bruchidae) penetrate the wall of the female genital tract to prevent re-mating of the female. (The “Bruchidae” are, in terms of phylogeny, simply a subtaxon of the Chrysomelidae, as discussed by SCHMITT 1996).

The latter works show impressively that studies on functional morphology of genitalia can provide new insights on sexual selection and sexual conflict. Our aim is to investigate the functional role of genital structures in all subfamilies of Chrysomelidae to learn more about these phenomena in the whole family. Hopefully, the results will lead to new ideas on speciation processes in this large beetle family. In this paper we present some first results gained from three species.

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[1] Paper presented to the 6th International Symposium on the Chrysomelidae, Bonn, Germany, May 7, 2004.

2. MATERIALS AND METHODS

2.1. Beetles

Bruchidae

Acanthoscelides obtectus (Say, 1831):

Breeding of these beetles is very uncomplicated, in which a preserving glass was used, filled with beans and with a lid consisting of a membrane permeable to air. We received seed-beetles from the Institute for Plant Diseases, Bonn and used the bush beans Montano or Maja as substrate. Every three months we removed dead beetles and replaced a portion of the old beans with fresh ones.

Chrysomelidae-Criocerinae

Lilioceris lilii (Scopoli, 1763):

These beetles were caught in private gardens around Bonn and Kevelaer (lower Rhine province near the Dutch border) in April and May 2003. We kept them in *Drosophila*-tubes, where they fed on leaves of *Lilium* sp. To achieve an improved climate, a layer of 1-2 cm of gypsum was poured into the bottom of the rearing tubes.

Oulema melanopus (Linnaeus, 1758)/ *Oulema duftschmidi* (Redtenbacher, 1874):

Specimens of *Oulema* came from a wheat field near Bonn in May 2003. They were kept in *Drosophila*-glasses like *L. lilii* and fed wheat plants from the native field. As the two species are only distinguishable by their genitalia and lack external differences, the first author caught and worked with both forms. The results for each species were pooled and therefore are presented as a whole and not seperately.

2.2. Behaviour

To initiate and observe copulations we put pairs or small groups of beetles together in a tube. The behaviour was visible with the naked eye. For some details we used a dissecting microscope. Ten copulations of different individuals of *A. obtectus* were watched closely. In Criocerinae we observed fewer copulations accurately from beginning to end ($n \leq 3$). Duration of copulation could be estimated by keeping an eye on the tubes while occupied with work elsewhere. We define copulation time as the time during which the aedeagus is inserted in the female.

2.3. Fixation in copula

To fix the copulating beetles we used chloroethyl spray (Chloraethyl "Dr. Hennig", Dr. Georg Friedrich Hennig, Chemische Fabrik Walldorf GmbH, D-69190 Walldorf, Germany). Shock freezing by this spray works well, but sometimes the, mating pairs separated partly or completely by the pressure of spraying. In these cases, the mates had not been coupled sufficiently. We fixed 8 – 12 pairs of each species. Frozen beetles were dissected or stored in 70% ethanol at –12 °C for three weeks.

2.4. Histology

After three weeks the entire beetles or their abdomina were transferred from 70% to 100% ethanol (30 min each in 80%, 90%, 95%, 100% ethanol). Each was immersed in a second soaking in 100% ethanol overnight. Resin was prepared with the "Low Viscositiy" set from Electron Microscopy Sciences (Hatfield, Pennsylvania). Objects were infiltrated by a further series (at intervals of 30 min aceton : resin 1:1, aceton : resin 1:3 and 60 min pure resin) and degased in an exsiccator. The Resin was put in silicon moulds (6x12x5 mm or 6x14x4 mm), the objects added and adjusted. The resin polymerised over night at 69 °C.

The embedded objects (1-3 in copula fixed pairs of each species) were cut with a microtome in slices of 1.0 µm or 1.5 µm. Every fifth section was put on a slide, heat-dried and dyed with Richardson-dilution (Böck 1989). To study the slices we used a Nikon Eclipse E600.

2.5. Scanning electron microscopy

We used the SEM to study in detail the shape and surface of the endophallus. Three exemplars, one of each species, were prepared from in copula-fixed pairs. Therefore, the endophallus was everted in an authentic way in all preparations. Objects were transferred from 70% to 100% ethanol and dried using HMDS (Hexamethyldisilazane) (Bock 1987). After fixing them on a stub they were coated with a 35 nm gold-layer using a HUMMER VII sputter (ANATECH LTD). We used an HITACHI S-2460 N SEM.

3. RESULTS

3.1. *Acanthoscelides obtectus*

Pairs of *A. obtectus* mate for about ten minutes. After this time, the male often leans backwards until it is almost lying on its back, after which it separates from the female. Females do not seem to be willing to remate directly after copulation but require a refractory period.

It is striking that fixed pairs separate very easily during dissection. The linking between the dead male and female is much less strong than in Criocerinae.

As shown in Figure 1, the parameres in *A. obtectus* remain outside the female and lay on the last female sternite during copulation while the median lobe is inserted. The photo is taken from a pair fixed in copula. One of us (SD) could observe this also while watching live individuals of *A. obtectus* through a dissecting microscope: The male moves the parameres up and down on the last female sternite during copulation and pushes only the tip of the median lobe into the female genital opening. Before inserting the median lobe, the male strikes the female genital opening with the setae of his parameres by moving them up and down.

In Figure 2, the considerable size of the everted endophallus is visible. It is formed like a balloon and fills the whole bursa copulatrix during copulation. The close-up view (Fig. 3) shows that the parameres are nearly flush with the median lobe. That means that even during copulation, the median lobe and tegmen are hardly moved against each other.

The surface of the endophallus bears teeth-like structures on its central region that are obviously sclerotised and appear quite sharp (Fig. 4). These teeth are absent on the apical region; in the basal region they are longer, less sharp structures.

3.2. *Oulema melanopus/duftschmidi*

In this species, pairing lasts longer than in *A. obtectus*. The males insert their median lobes for about twenty minutes or even longer. After copulation, males continue to sit on the females' elytra, guarding their mates. Females try to get rid of them by kicking. Both sexes may remate directly after copulation.

The endophallus of *O. duftschmidi* consists of a membranous and a sclerotised part, the so-called flagellum (Fig. 5). The flagellum is tubular, at least apically (Fig. 6). During copulation, the median lobe is inserted completely in *O. melanopus*. The endophallus fills the whole bursa copulatrix (Fig. 7). A close-up view (Fig. 8) shows how well the walls of bursa and endophallus match. Every bulge of the bursa is filled by the endophallus. Figure 8 shows clearly that not only the distal part of the flagellum is tubular but also the whole structure is tubular. An analysis of the neighbouring sections revealed that the flagellum ends at the entrance of the spermathecal duct.

The surface of the endophallus of *O. duftschmidi* bears comb-like structures (Fig. 9) or something similar. They are not sclerotised, unlike the "teeth" of *A. obtectus*. The structures are directed towards the median lobe.

3.3. *Lilioceris lilii*

As in *O. melanopus*, copulation in *L. lilii* takes more than twenty minutes. The male clings to the female's back for several hours while the male organ is intromitted.

The everted endophallus of *L. lilii* is about three times the diameter of the median lobe (Fig. 10). This fact obviously facilitates a perfect mechanical coupling of *Lilioceris*-pairs. The fixed pairs could hardly be separated. As in *Oulema*, the endophallus is divided into a membranous and sclerotised part. The sclerotised part includes the flagellum as one can see in the SEM photo (Fig. 11). The tip of the flagellum is also tubular (Fig. 12).

The sagittal section of *Lilioceris* (Fig. 13) represents the mates during copulation. Even if one cannot see a connection between the male body and the median lobe in this figure, one can imagine that the median lobe is inserted. The endophallus fills the bursa. The sclerotised part of the endophallus is visible lying close to the basal part of the spermatheca. We can track this on the preceding and following sections. Thus, in *L. lilii* as well as in *O. melanopus* the tip of the flagellum is positioned very close to the entrance of the spermatheca.

The surface of the endophallus of *L. lilii* bears the same comb-like structures as *O. duftschmidi*. But there are additional structures in *L. lilii* (Fig. 14), closely resembling sensilla campaniformia, receptors responding to pressure. These receptors occur in rows on parts of the surface of the endophallus. After we had found these structures we searched for dendrites in the sections. And indeed, we found structures crossing the wall of the endophallus, which could be interpreted as dendrites.

4. DISCUSSION

4.1. General aspects

We focused on three species that were easily available. Furthermore, we decided to work with one species possessing parameres and two species without in order to obtain an idea on the functional role of these structures. We chose closely related species to enable a meaningful comparison.

In future studies, the methods will be maintained but have to be expanded. Paraffin sections for example will be necessary to demonstrate sperm by giemsa-staining. In our sections we found structures inside the flagellum of *Oulema* that seem to be spermatozoa, however we are presently uncertain. Besides that, many more pairs of each species will have to be fixed for a comparison of different states of copulation. This will permit us to reconstruct the process of copulation.

4.2. Sperm-transfer

We assume that in *L. lilii* and *O. melanopus/duftschmidi* the flagellum is positioned near the spermatheca to guarantee a directed sperm transfer towards the female sperm-storage. The results show that the flagellum in *O.*

melanopus/duftschmidi as well as in *L. lilii* is tubular with a distal opening. Therefore, one could imagine that it is involved in sperm transfer. BERTI & RAPILLY (1976) studied the endophallus of *L. lilii* under a taxonomic aspect and figured the ejaculatory duct ending in the flagellum tube. That means that in *L. lilii* sperm transfer actually takes place through the tubular flagellum. It is self-evident that the same may be the case in *O. melanopus/duftschmidi*, though we have not found the ejaculatory duct in the sections. The idea of the flagellum as a sperm transferring structure is corroborated by the positioning of its tip: the males presumably adduct their flagellum close to the basal piece of the spermatheca to increase the probability that their sperm arrives at the entrance. RODRIGUEZ et al. (2004) consider possible that the flagellum of *Chelymorpha alternans* (Chrysomelidae: Cassidinae) is pushed up into the spermathecal duct to release sperm there. Tactics of males to transport their sperm close to or even into the spermatheca have been investigated in other cases as well, for example in the staphylinid *Aleochora curtula* (GACK & PESCHKE 1994). It is conceivable that the long and thin flagellum of *O. duftschmidi* may reach even into the spermathecal duct during copulation. The spermathecal duct of this form is longer than in *O. melanopus* (BERTI 1989). One could suppose that females have in the course of evolution lengthened the distance from the spermatheca to test the males` quality. Males responded by extending their flagellum. In *Chelymorpha* species (RODRÍGUEZ et al. 2004) the length of the flagellum is actually adapted to the length of the spermathecal duct. Females of this species prefer males with a longer flagellum that reaches the spermatheca.

The question if *L. lilii* and *O. melanopus/duftschmidi* form spermatophores as well, is unsolved so far as for many other Chrysomelidae. Males of *C. alternans* transmit a spermatophore in addition to the pretended sperm transfer via the flagellum (RODRÍGUEZ et al 2004). In the Criocerinae we have so far not found any trace of a spermatophore in the sections (which does not necessarily mean that spermathophores do not exist). Males of *Acanthoscelides obtectus* are able to produce a spermatophore (HUIGNARD 1978, 1983), which we also could identify in the sections.

It is an open question if Criocerinae males remove previous males' sperm by means of their genitalia, as males in many other groups do (HAUBRUGE et al. 1999; FREITAG et al. 2001). It can't be excluded that the flagellum has this additional function. In *Acanthoscelides,* it is improbable that the males dispose other males' sperm from the female genital tract because the median lobe is hardly inserted and no structures of the endophallus seem to be able to perform such a function.

4.3. Parameres

HARNISCH (1915) has already observed that in *Plateumaris sericea* (Chrysomelidae: Donaciinae) the parameres remain outside the female genitalia. He suggests that they act as a grasping organ to connect the male more intensively to the female during copulation. Our results show that the parameres of *A. obtectus* can't fulfill this function because the lever formed by them is too short to stabilize. Another possible function of the parameres is to position the apical orifice of the median lobe opposite the opening of the female genital tract as KINGSOLVER (1970) suggests. SD observed in live *A. obtectus* individuals that the male touched the female genital area with the setae of the parameres before inserting the median lobe. It is hard to decide if this touching serves the male to orientate the position of the median lobe or to stimulate the female. Such kind of paramere-movement has been observed in other groups as well: males of the carabid beetle *Pasimachus punctulatus* tap their parameres rhythmically upon the apical edge of the female last abdominal sternite. After a while, the genital orifice of the female opens and the male inserts his median lobe (ALEXANDER 1959). If these movements actually serve as stimulation, this would support the cryptic female choice hypothesis (EBERHARD 1985).

4.4. Surface of the Endophallus

The comb-like structures on the surface of the endophallus in *L. lilii* and *O. duftschmidi* are directed towards the median lobe. We assume that the functional role of these structures is to support the mechanical coupling of the mates. They may make it more difficult to disconnect the median lobe forcibly out of the bursa or without the agreement of the male, respectively. If the females want to stop copulation and get rid of the aedeagus, they use their legs to kick the male away as is common for many other species of Chrysomelidae as well (DICKINSON 1997; JOLIVET 1999; CRUDGINGTON & SIVA-JOTHY 2000). The everted matching endophallus with its microstructures may prevent separation. Another possible function of the ultrastructures of the endophallus may be stimulatory. To verify this idea there should be receptors on the interior wall of the bursa copulatrix.

The other structures on the endophallus of *L. lilii* are without much doubt receptors. The existence of such receptors means probably that the males are able to control the eversion and positioning of the endophallus very well. The sensilla campaniformia may sense that correct position inside the bursa to provide the best opportunity for the flagellum to perform direct sperm transfer.

Acanthoscelides obtectus males have teeth-like structures on the surface of their endophallus. KINGSOLVER (1970) suggests that these structures or "endophallus armature" serve as holding devices during copulation. This seems to be a good idea, especially because the shape of the endophallus of *A. obtectus* is not suitable to guarantee its foothold inside the female. But in contrast to the little combs in the Criocerinae, the structures in *A. obtectus* are sclerotized and may have another function as well. CRUDGINGTON & SIVA JOTHY (2000) found that the armed endophallus of *Callosobruchus maculatus* penetrates the bursa wall during copulation. This damage of the genital tract is costly for the female because it has to repair the wall. The study even points out that copulation frequency has a life-history cost for females: doubly mated females died significantly younger than singly mated females. Hurting the female is thus a strategy of males to ensure that females will not remate. Maybe the same is the case in *A. obtectus*. As our observations of live individuals showed, females of *A. obtectus* do not remate after copulation for a fairly long time (unlike females of *O. melanopus*). To reach clarity, we shall have to analyse the bursa wall after copulation.

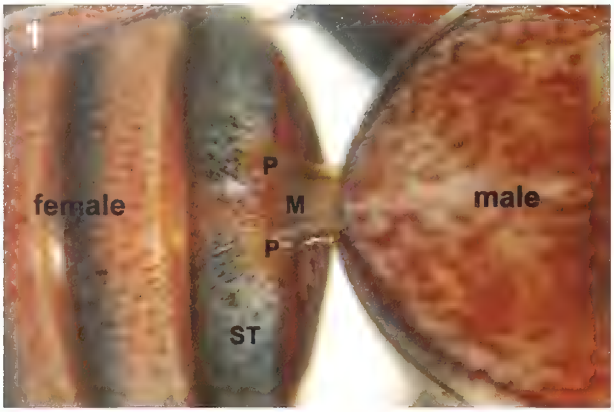
4.5. Perspectives for evolutionary biology

The results show that the males of *A. obtectus* on one side and the Criocerinae on the other embark on different strategies. In Criocerinae, the males try to prevent further copulations of the females by mate guarding. They obviously have no additional strategy because females seem to be willing to remate just after copulation if only the males desist from them. In *A. obtectus*, the males do not stay longer on the females than copulation or even the pure transfer of the spermatophore lasts. They do not spend as much time in pairing than the Criocerinae but have a different way to prohibit a remate of the females. As HUIGNARD (1983) described, the deposition of the spermatophore in *A. obtectus* is followed "by stimulation of oogenesis and egg-laying, as well as by a temporary inhibition of female receptivity". He ascertained that male secretions are transferred from the spermatophore into the female haemolymph through the wall of the bursa. It is uncleared if these secretions are the main cause of the refractory period of the females or if damage of the bursa wall like in *C. maculatus* (CRUDGINGTON & SIVA-JOTHY 2000) is an additional male strategy to inhibit a female remating. If there will be no damages in the bursa detectable after copulation, we have to ask for another function of the teeth on the endophallus surface. We then will agree with KINGSOLVER 1970 that they mainly serve as holding devices.

Males in Criocerinae obviously achieve the mechanical coupling with their voluminous inflated endophallus and its additional microstructures. So, if the mechanical coupling in Donaciinae is achieved by the parameres as grasping organs (HARNISCH 1915), it would be interesting to know if their endophallus is less voluminous and possesses no microstructures. An idea could be that all species without anchoring parameres offer a voluminous endophallus or at least an endophallus with holding microstructures.

One could speculate that there exist three types of Chrysomelidae – one without parameres, another with parameres that serve mainly as grasping organs, and a third that uses the parameres for orientation or stimulation.

Acknowledgements. We thank Dr. Bernhard Huber (Bonn) for help in all histological matters, Lasse Hubweber (Bonn) for stimulating discussions, Karin Ulmen (Bonn) for technical assistance at the SEM, Bradley J. Sinclair (Bonn) for linguistic assistance, Sandra Steiger (Freiburg im Breisgau) for her patience in searching for dendrite-like-structures in the sections and two anonymous referees for valuable input.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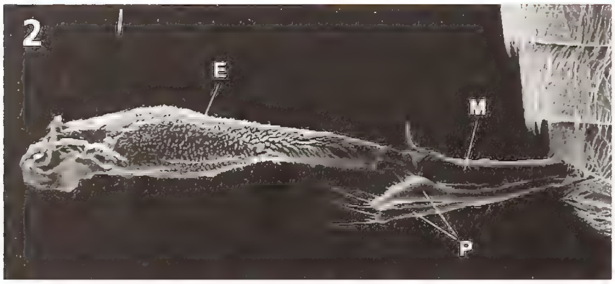
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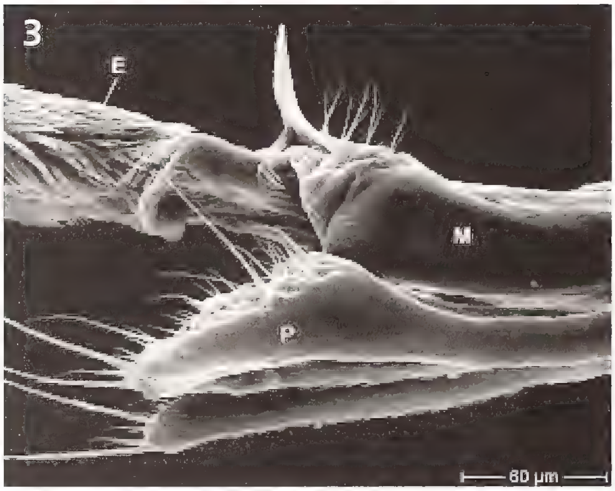
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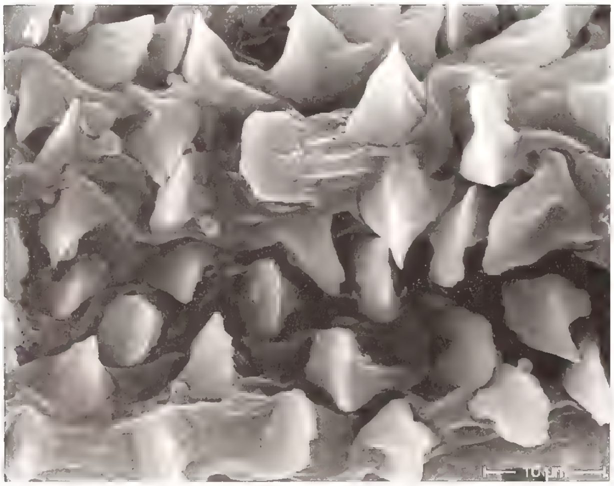
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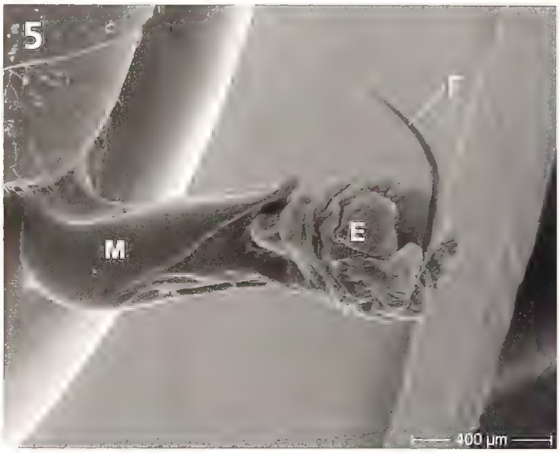
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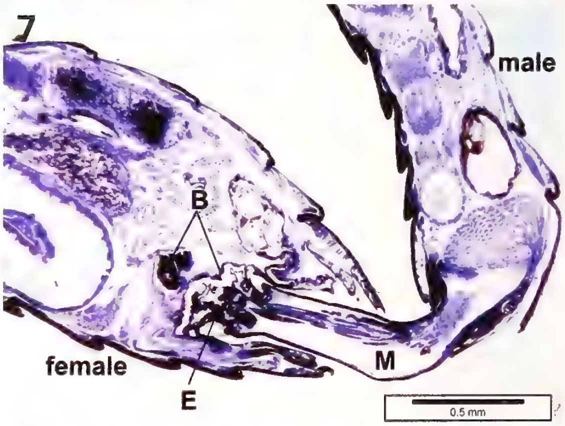
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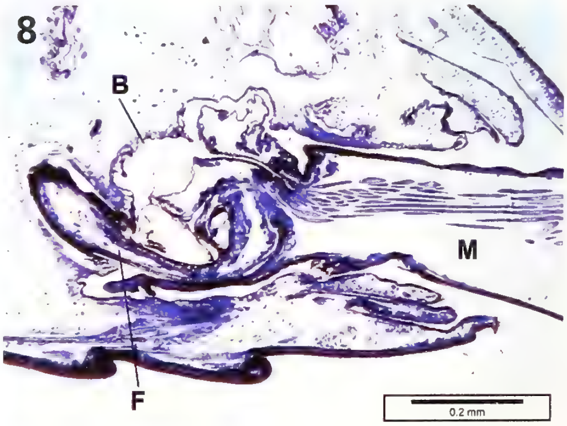
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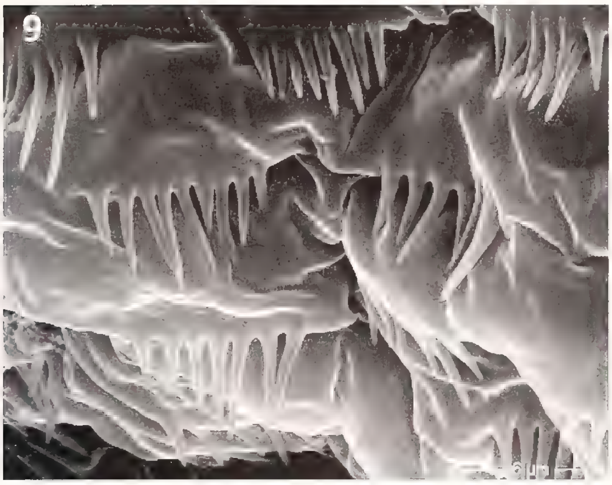

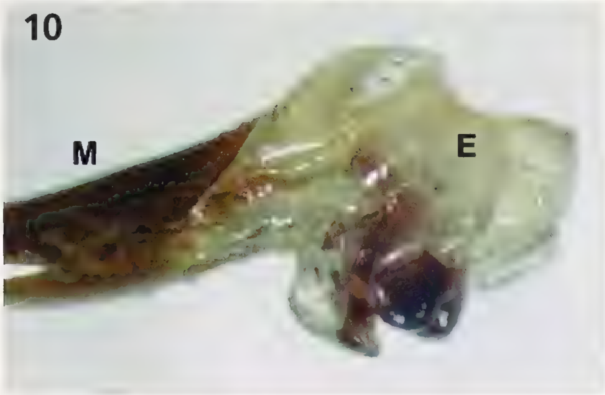

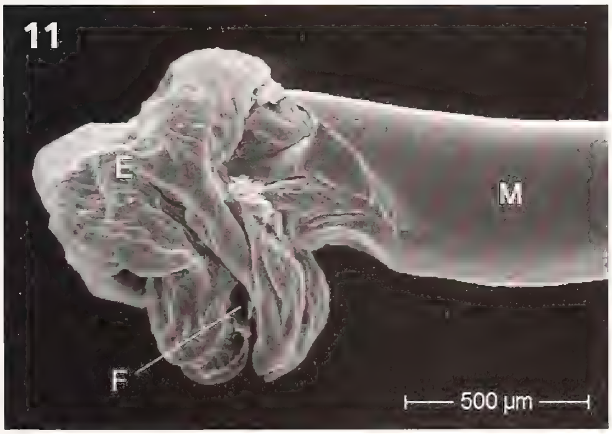

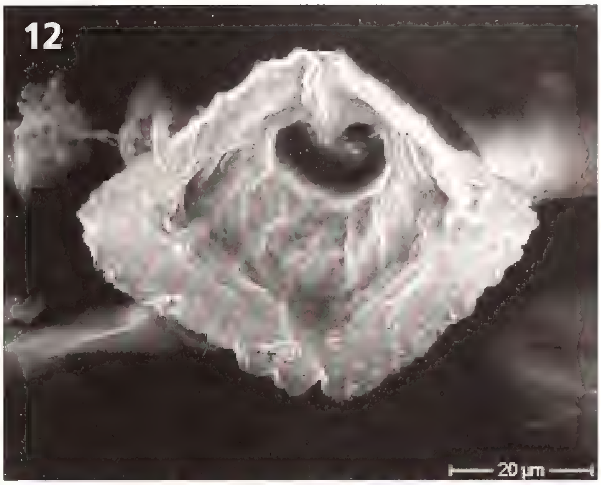

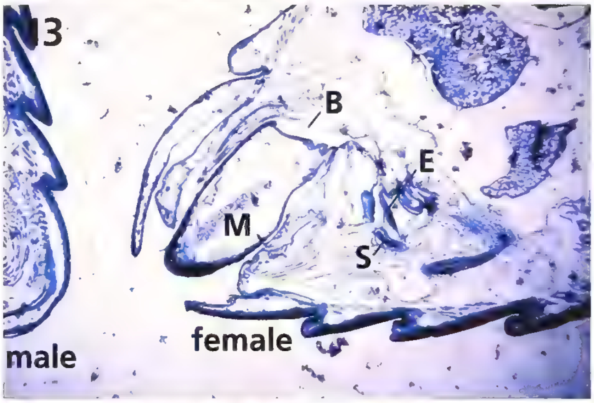

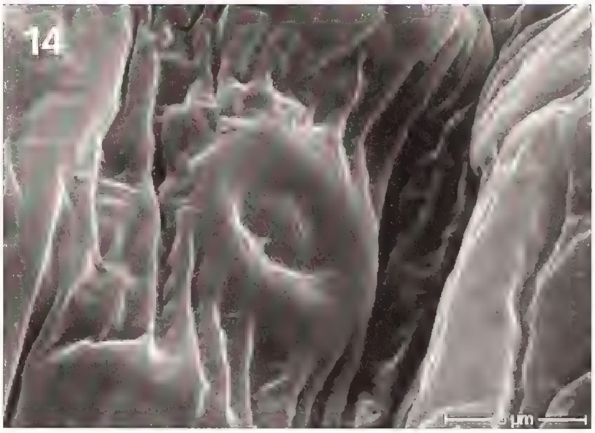

Fig. 1. Ventral view of a copulating pair of *Acanthoscelides obtectus,* fixed by chloroethyl spray. P: parameres, M: median lobe, ST: last female sternite. Stereomicrograph. – **Fig. 2.** *A. obtectus.* Aedeagus with everted endophallus (E). M: median lobe, P: parameres. Scanning electron micrograph. – **Fig. 3.** *A. obtectus.* Close-up view of the aedeagus. E: endophallus, M: median lobe, P: parameres. Scanning electron micrograph. – **Fig. 4.** *A. obtecuts.* Surface of the endophallus. Scanning electron micrograph. – **Fig. 5.** Aedeagus of *Oulema duftschmidi.* E: endophallus, F: flagellum, M: median lobe. Scanning electron micrograph. – **Fig. 6.** *O. duftschmidi.* Tip of the flagellum. Scanning electron micrograph. – **Fig. 7.** Sagittal section of *O. melanopus* in copula. B: bursa copulatrix, E: endophallus, M: median lobe. Micrograph. – **Fig. 8.** Sagittal section of *O. melanopus* in copula. B: bursa copulatrix, F: flagellum, M: median lobe. Micrograph. – **Fig. 9.** *O. duftschmidi.* Surface of the endophallus. Scanning electron micrograph. – **Fig. 10.** Dissected aedeagus of *Lilioceris lilii.* E: endophallus, M: median lobe. Stereomicrograph. – **Fig. 11.** *L. lilii.* The sclerotised part of the endophallus (E) bears the flagellum (F). M: median lobe. Scanning electron micrograph. – **Fig. 12.** *L. lilii.* Tip of the flagellum. Scanning electron micrograph. – **Fig. 13.** Sagittal section of *L. lilii* in copula. B: bursa copulatrix, E: endophallus, M: median lobe, S: spermatheca. Micrograph. – **Fig. 14.** Campaniform sensillum on the surface of the endophallus of *L .lilii.* Scanning electron micrograph.

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Bonner zoologische Beiträge	Band 54 (2005)	Heft 4	Seiten 209–237	Bonn, Oktober 2006

The Current Status of Knowledge of the Alticinae of Mexico (Coleoptera: Chrysomelidae)[1]

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Abstract. The current state of knowledge of the diversity for Alticinae recorded from Mexico is taken from the historical literature, determined specimens primarily in the U.S. National Museum, including material collected by the author, as well as from several other institutions. An Appendix is provided containing a list of generic and specific names recorded from Mexico, including the known distribution for each species by Mexican state and the source for that information. There are 89 genera and 524 species currently known from Mexico. Although preliminary, this is a significant increase from the published literature. The Alticinae species diversity per Mexican state is also provided. Some discussion of the Mexican Alticinae biogeographic affinities is given. The following changes in status are made: *Syphrea bibiana* Bechyné = *Nesaecrepida infuscata* (Schaeffer); *Palaeothona* Jacoby is raised from synonymy with *Lupraea* Jacoby and considered valid; *Varicoxa* Bechyné = *Luperaltica* Crotch; *Kuschelina gracilis* Jacoby is raised from synonymy with *K. laeta* (Perbosc) and considered valid; *Aphthona dimidiaticornis* Jacoby, *A. fulvipennis* Jacoby, *A. maculipennis* Jacoby, *A. mexicana* (Jacoby), *A. pallipes* (Jacoby), *A. semipunctata* Jacoby, and *A. substriata* Jacoby are all considered to be in *Centralaphthona* Bechyné; *Aphthona amulensis* Jacoby = *Genaphthona* Bechyné; *Aphthona fulvitarsis* Jacoby = *Gioia* Bechyné; *A. championi* Jacoby = *Lupraea*.

Keywords. Alticinae, flea beetles, Chrysomelidae, Mexico, biogeography

1. INTRODUCTION

Mexico is the largest part (ca. 50%) of the Mesoamerican biodiversity "hotspot" which is second in species diversity and endemism of the top 25 "hotspots" in the world (MITTERMEIER et al. 1999). It has been called one of the world's "megadiversity" countries (MITTERMEIER 1988) and ranks third in this respect according to some. Mexico is situated in a biogeographic transition zone between the Nearctic Region to the north and the Neotropical Region to the south. Generally in Mexico the Nearctic biotic elements are in the northern areas, the central arid plateau with some arid elements reaching as far south as Oaxaca. The Neotropical elements are in the south with some elements reaching along the coasts to Tamaulipas in the east and to southern Sinaloa in the west. Species diversity/richness has been documented to be very high in many well-known groups, such as plants (RZEDOWSKI 1993, 1996), mammals (FA & MORALES 1993; MITTERMEIER et al. 1999), and butterflies (LLORENTE & MARTÍNEZ 1993, LLORENTE et al. 1996). Species diversity also varies from group to group and from state to state. The highest diversity generally occurs in the more tropical states such as Chiapas, Oaxaca and Vera Cruz. Some examples of this from the insect world include Odonata (GONZÁLEZ & NOVELO 1996), Pscoptera (MOCKFORD & GARCÍA ALDRETE 1996), Passalidae (REYES-CASTILLO 2002), Bruchidae with Jalisco and Morelos also high (NÁPOLES 2002).

Because of this biogeographic transition zone between the Nearctic and Neotropical Regions, biogeographic affinities may also vary greatly depending on the group considered. Examples of this in the Coleoptera are species of Curculionidae with 41% Neotropical and 14% Nearctic affinities (ANDERSON & O'BRIEN 1996) and Carabidae with 54% Nearctic and 14% Neotropical, but in generic affinities 40% are Neotropical and 20% are Nearctic (BALL & SHPELEY 2000).

Levels of endemism vary greatly depending on the group considered and, of course, depending on the relative knowledge of the group. As with any country some vertebrate and plant groups are well know, whereas most insect groups are not. In mammals about 32% of the species are endemic (FA & MORALES 1993) and in the phanerogamic plants 10% of the genera and 52% of the species are endemic (RZEDOWSKI 1993). Among the insects butterflies are well-known, yet in Mexico the Papilionidae have only 10% endemism there (LLORENTE & MARTÍNEZ 1993). For native bees the level of endemism ranges from 25-60% depending on the region of Mexico, both the tropical state of Vera Cruz and the north of Baja California have 30%, whereas Guerrero has 50% and the Balsas (Guerrero-Oaxaca) has almost 60% (AYALA et al. 1993). Species endemism is generally high, but may vary, for example, in Homoptera it varies from 4% in Membracidae to 63% in Aleyrodidae (O'BRIEN et al. 1996), Pscoptera 74% (MOCKFORD & GARCÍA ALDRETE 1996), Carabidae 60% (Ball & Shpeley 2000), Tenebrionidae 52% (AALBU et al. 2002), Curculionidae 40.5% (ANDERSON & O'BRIEN 1996).

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[1] Paper presented to the 6th International Symposium on the Chrysomelidae, Bonn, Germany, May 7, 2004

Nearctic Alticinae (ca. 40 genera) are reasonably well known at the genus and species level in comparison to the Neotropical taxa (over 200 genera); however, there are certainly many more new species to be discovered there. Recently there was an update of the treatment at the genus level (RILEY et al. 2002) including keys. RILEY et al. (2003) have published a detailed checklist to the Nearctic Chrysomelidae. Neotropical Alticinae have been recently treated in a number of references by J. and B. BECHYNÉ (see References), D. BLAKE (see References), WILCOX (1975), SCHERER (1983), FURTH & SAVINI (1996, 1998), FURTH et al. (2003), and FURTH (2004). Almost half of the known Alticinae genera occur in the Neotropics; about 230 generic names were listed in SCHERER (1983) about 90 of which were described by Jan and Bohumila Bechyné.

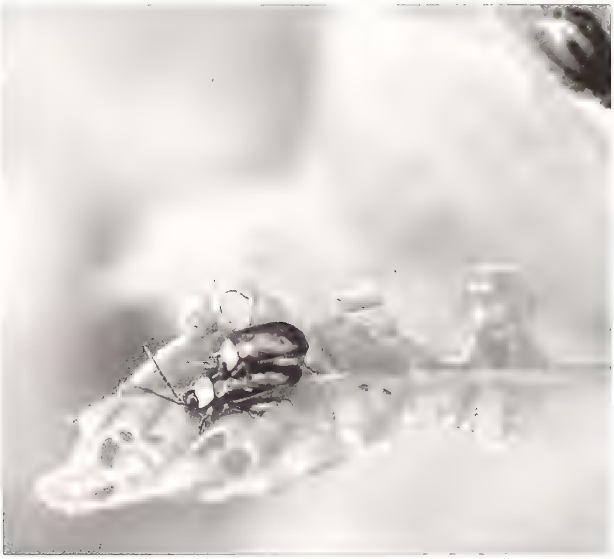


Fig. 1. *Asphaera abdominalis* (Chevrolat) on *Ludwigia peploides* (Kunth) Raven, in copula, Zacatecas, July 1995. (Photo: D. Furth).

In the historical literature (Tables 1 and 2), JACOBY in the Biologia Centrali Americana (1884-1892) listed 334 species in 50 genera from Mexico, many of these genera and species were listed under old names that were later changed. HEIKERTINGER & CSIKI (1939-40) added 23 species and three genera *Argopistes* Motschulsky, *Blepharonycha* (Fall) and *Heikertingerella* (Csiki). BLACKWELDER (1946) added 12 species (9 from Baja California) and four genera: *Distigmoptera* (Blake); *Glyptina* (LeConte); *Dysphenges* (Horn); *Euplectroscelis* (Crotch) – the first to correctly clarify this genus. From more recent literature, FURTH & SAVINI (1996) listed 400 species in 74 genera. FURTH & SAVINI (1998) added 1 genus and 11 species. FURTH (1998) added 18 species of *Blepharida* Chevrolat and synonymized *Blepharonycha* as well as 3 species of *Blepharida* (s.s) (see Table 1). RILEY et al. (2001) placed *Hornaltica atriventris* (Melsheimer) in *Margaridisa*, thus eliminating the former as a separate genus known from Mexico and they raised *Hemiphyrnus* Horn out of synonymy with *Phyrnocepha* Baly, thus adding another genus name to the Mexican checklist. FURTH (2004) added 11 genera and 69 species to the Mexican fauna.

Mexico is a very large country, 14th largest in the world, so one would expect a high diversity of species compared to smaller countries in Central America. There are about 350 species in 89 genera currently known from Costa Rica, particularly because of some recent intensive quantitative inventorying done at a single site (FURTH et al. 2003). In contrast, in the smaller and less surveyed Panama, there are only 270 species in 70 genera known (FURTH & SAVINI 1996, 1998).

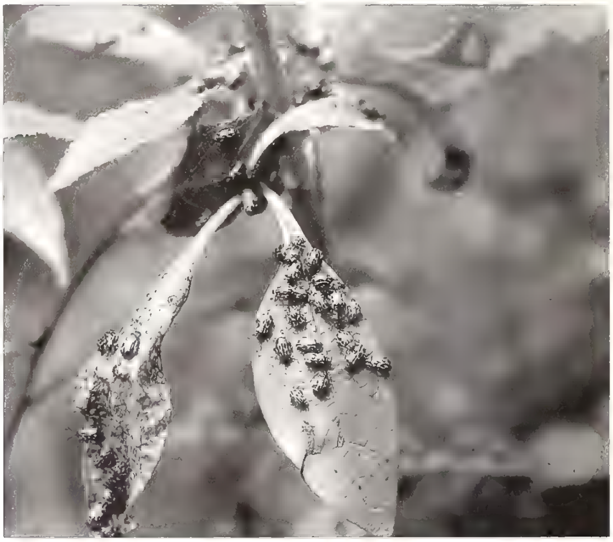


Fig. 2. *Capraita conspurcata* (Jacoby), Morelos, June 1993. (Photo: D. Furth).

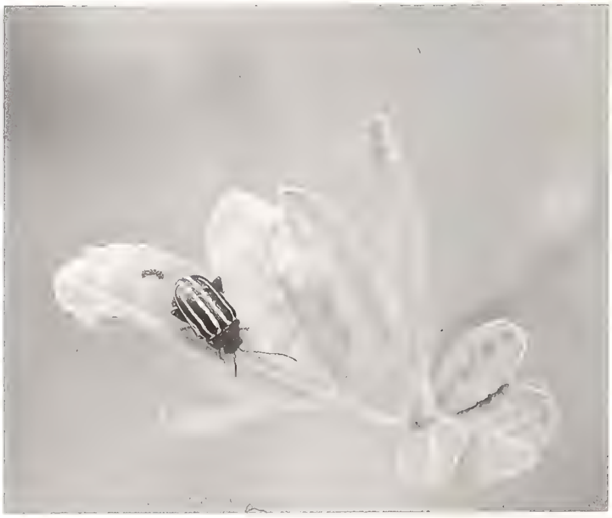


Fig. 3. *Blepharida lineata* Furth on *Bursera trimera* Bullock, Guerrero, June 1993. (Photo: D. Furth).

Table 1. Numbers of historical and current Mexican Alticinae species

Genus	Species	Source
74	400	FURTH & SAVINI (1996)
1	11 (-1)	FURTH & SAVINI (1998)
-1	18 (-3)	FURTH (1998)
1	3	SAVINI et al. (2001)
-1(1)	0	RILEY et al. (2001)
0	3	GILBERT & ANDREWS (2002)
9	32	FURTH (2004) – USNM
3	12	FURTH (2004) – USNM-DGF
0	25	FURTH (2004) – MCZC-FCB
-1	4 (-3)	Corrections to FURTH & SAVINI (1996)
4(-1)	21	NEW – this study
89	524	Total

Table 2. Mexican Alticinae Genera – old and new records

Genera	General Distribution	Source (Mexico)
73	Mexico, etc.	FURTH & SAVINI (1996)
"*Crepidodera*"	Mexico (Baja California)	FURTH & SAVINI (1998)
- (*Blepharonycha*)	Mexico	FURTH (1998)
Gioia	Brazil, Venezuela, Colombia, Ecuador, Guadeloupe, Panama, Costa Rica	SAVINI et al. (2001)
Hemiphyrnus	USA, Mexico	RILEY et al. (2001)
-/+ *Hornaltica*	USA	RILEY et al. (2001)
Ayalaia	El Salvador	FURTH (2004) – USNM
Chalatenanganya	Venezuela, Trinidad, El Salvador, Guatemala, Costa Rica	FURTH (2004) – USNM-DGF
Egleraltica	Brazil, Venezuela, Costa Rica	FURTH (2004) – USNM
Exoceras	Brazil, Bolivia, Venezuela, Trinidad, St. Vincent, St. Lucia, Dominica, Guadeloupe, Puerto Rico, Dominican Republic, Haiti, Jamaica, Cuba, Panama, Costa Rica	FURTH (2004) – USNM
Genaphthona	Brazil, Paraguay, Bolivia, Venezuela, El Salvador, Costa Rica, Guatemala,	FURTH (2004) – USNM
Leptophysa	Brazil, Paraguay, Venezuela, Jamaica, Panama, Costa Rica	FURTH (2004) – USNM
Margaridisa	Brazil, Venezuela, Costa Rica, Nicaragua	FURTH (2004) – USNM
Neothona	Venezuela, Trinidad, El Salvador, Costa Rica	FURTH (2004) – USNM
Nesaecrepida	USA, Jamaica, Cuba, Puerto Rico	FURTH (2004) – USNM-DGF
Terpnochlorus	Venezuela, Madagascar	FURTH (2004) – USNM
Tetragonotes	Brazil, Bolivia, Peru, Ecuador, Colombia, Venezuela, Panama, Costa Rica, Nicaragua, Guatemala	FURTH (2004) – USNM
Deuteraltica	Guatemala, El Salvador	USNM – New
Heikertingeria	Guatemala,Panama,Venezuela, Bolivia, Peru, Brazil,Trinidad	USNM – New
Luperaltica	USA, C. & S. America	USNM – New
Palaeothona	C. & S. America	New
- *Varicoxa*	C. & S. America	New
89		**Total**

Ashpaera abdominalis (Chevrolat) (Fig. 1) is one of the most common species in Mexico and, in fact in all of Central America. Another common species in Mexico is *Capraita conspurcatus* (Jacoby) (Fig. 2) that is often found in very large numbers and may completely destroy its host plants. New World *Blepharida* were monographed by FURTH (1998) and of the 38 species, 31 are endemic to Mexico and all but 2 can be found in Mexico. Some species are apparently oliphagous and are recorded on several species of *Bursera* (FURTH 1998); however, most species are monophagous on species of *Bursera* (Burseraceae), such as *B. lineata* (Fig. 3).

2. METHODS

Records of Mexican Alticinae were recovered in several ways for the current study. First a search of published literature, especially the references in FURTH & SAVINI (1996, 1998) as well as more recent publications, was made and the locality data for the Mexican states checked. The identified and unidentified collections of the National Museum of Natural History (Smithsonian Institution) (USNM) were checked for Mexican state records using a recent species inventory funded by the Smithsonian Women's Committee. The author determined many of the unidentified Mexican Alticinae specimens at the USNM. Additional Mexican state distribution data was extracted from the F. C. Bowditch Collection (FCB) previously on long-term loan to the author from the Museum of Comparative Zoology (Harvard University – MCZC). Also some material collected and determined by the author in Mexico was included (USNM-DGF). Finally some records from a recent visit to the Naturhistorisches Museum Basel (Switzerland) (NHMB) and the Zoologisches Staatssammlungen München (Germany) (ZSMC) were also incorporated. Some representative specimens will be deposited at the Colección Nacional de Insectos, Instituto de Biología, Universidad Autonoma de Mexico (UNAM-IB).

3. RESULTS

3.1. General

The Appendix contains the most up-to-date checklist of Mexican Alticinae with distributional information at the Mexican state level and a number of new synonymies, new combinations and other name changes (see below). Since FURTH (2004) the author has discovered three additional genera and 21 species to the Mexican fauna. Five species recorded in the historical literature only as "Mexico" have been more specifically recorded in particular Mexican states. Thus, the total Alticinae diversity of Mexico consists of 89 genera and 524 species (Tables 1 & 2).

3.2. New synonymy and other nomenclatural changes

During the course of this project the author has discovered several notable new synonymies and other name changes that should be clarified in order to facilitate the consistent usage of the names of Neotropical Alticinae, especially Mexican Alticinae.

Syphrea bibiana Bechyné was described by BECHYNÉ (1955) from British Honduras. The author has examined the holotype and type series in the Frey Collection at NHMB and finds that it is conspecific with *Nesaecrepida infuscata* (Schaeffer) [combination established by RILEY et al. 2001]. SCHAEFFER (1906) described this species from a single specimen from Brownsville, Texas, deposited in the USNM and the author has also examined this holotype specimen. SCHAEFFER (1906) described this species as *Lactica infuscatus* and included a key to the three species of the genus, including *L. brumeliae* Schaeffer and *L. tibialis* Olivier. *Lactica* Erichson is currently considered to be a synonym of *Monomacra* Chevrolat. *Lactica brumeliae* is currently considered to be in the genus *Monomacra* and *L. tibialis* in the genus *Parchicola* Bechyné (RILEY et al. 2003). All of these species share a rather deeply impressed, transverse subbasal impression on the pronotum and this is no doubt why SCHAEFFER assumed they were congeneric. However, BLAKE (1964) accurately established the genus *Nesaecrepida* (type species *N. asphaltina* (Suffrian)) from Cuba and differentiated it from other "Crepidoderini" by having inconspicuous elytral punctation consisting of many fine striae. She also pointed out that the prebasal transverse impression extends completely across to the lateral margins of the pronotum without the usual limiting lines perpendicular to the base. This feature is also characteristic of *Syphrea* Baly and is probably the primary reason that Bechyné placed this species (as *S. bibiana*) in that genus. *Nesaecrepida* and *Syphrea* share some characteristics such as, base of the pronotum somewhat doubly sinuate, convex pronotum. They differ in the shape of the epipleura (usually not straight, gently emarginate in *Syphrea*), antennal bossae of *Nesaecrepida* small round (usually larger and not round in *Syphrea*) divided by base of the long narrow frontal ridge. Further characteristics of *Nesaecrepida infuscata* are: pronotum with anterolateral angles rounded, thickened and not distinctly angled, punctation dense, fine; dorsum light brown-yellow in color with elytral suture distinctly darkened, elytral punctures coarse, dense, not evidently striate; epipleura rather wide and parallel-sided, tapering only subapically.

This species has recently been studied as a potential biological control agent for *Mimosa pigra* Linnaeus (Mimosaceae) in Australia (W. Forno, Brisbane, pers. comm. 1992).

BECHYNÉ & BECHYNÉ (1960:23-24) first designated *Palaeothona* Jacoby (1885:377) [type species: *P. rugifrons* Jacoby, designated by BLAKE (1950:179)] as synonymous with *Lupraea* Jacoby (1885:359) [type species: *L. longicornis* Jacoby, designated by BECHYNÉ & BECHYNÉ (1960:24)]. The author has examined syntypes of *Lupraea longicornis* as well as of *Palaeothona rugifrons* and has determined that these two genera are in fact distinct as originally described by JACOBY (1885). BLAKE (1950) described four new species of *Palaeothona* from the USA, Mexico and Haiti and newly combined *Trachymetopa* (misspelled in BLAKE 1950 as *Trachymetropa* Weise) *picta* (Say) into *Palaeothona*. *Palaeothona picta* (Say) was originally described as *Altica* Geoffroy, then placed in *Aphthona* Chevrolat by CROTCH (1873), an then in *Phyllotreta* Chevrolat by HORN (1889). In fact in his original description of the genus Jacoby compared *Palaeothona* to *Aphthona* and even to *Phyllotreta*, but acknowledged that characters to distinguish it as a separate genus were not obvious. While *Palaeothona* and *Lupraea* Jacoby have some similarities, the differences are more evident (Vilma P. Savini, Maracay, Venezuela, *in litteris*): *Palaeothona* has a more convex and robust body form; *Lupraea* has antennomere 2 almost moniliform, much less than half the length of segment 3, *Palaeothona* has a relatively longer second antennomere, more than half the length of segment 3; *Lupraea* epipleura usually narrow throughout most of its length, not much wider than the first antennomere, gradually tapered apically, epipleura of *Palaeothona* wider throughout its length, tapered only subapically; eyes larger in most *Lupraea*; pronotum of *Palaeothona* with broad mid-basal depression; pronotal shape more elongate and evidently narrowed basally with anterolateral angles evenly rounded in *Lupraea* opposed to often angulate in *Palaeothona;* elytral bossae usually more pronounced in *Palaeothona*; elytral punctation denser and coarser in most *Lupraea*; antennal bossae small narrow, rounded or vertically aligned in *Palaeothona,* but horizontal, transverse or rectangular in *Lupraea*; antennae long, often as long or longer than body in *Lupraea*, shorter in *Palaeothona*; dorsum rather flattened in *Lupraea* and more convex in *Palaeothona*; pronotum and vertex of *Lupraea* usually smooth and impunctate, but usually at least vertex distinctly punctured or subrugose in *Palaeothona*; elytral punctation often coarser and denser in *Lupraea*. Most Mexican species were described as *Palaeothona* by Jacoby, but he also confused these two genera and so it is necessary to examine type specimens of each species in order to correctly place each in the correct genus. The author has been able to examine types of some, but not all of the Mexican species and, thus, verifies the placement of these as follows: *Palaeothona discrepans* (Schaeffer); *Lupraea elongata* (Jacoby); *Lupraea fulvicollis* Jacoby; *Lupraea godmani* (Jacoby); *Lupraea guatemalensis* (Jacoby); *Lupraea imitans* (Jacoby); *Palaeothona melanocyanea* Blake; *Palaeothona rubroviridis* Blake; *Palaeothona rugifrons* Jacoby; *Lupraea semifulva* (Jacoby); *Lupraea smithi* (Jacoby); *Palaeothona viridis* Jacoby. *Lupraea occipitalis* Bechyné & Bechyné is problematic and does not seem to fit in either genus well, but the author prefers to leave it in its current status until it can be studied in more detail. However, *Palaeothona dilaticornis* Jacoby and *Palaeothona frontalis* Jacoby are left in their originally described genus until their types can be studied. Therefore, the species here placed in *Palaeothona* are given a new status from recent publications (e.g., SAVINI & FURTH 1996, 1998; Riley et al. 2003; and FURTH 2004).

CROTCH (1873:70) established *Luperaltica* [type species: *L. senilis* (Say) designated by WILCOX (1953:54)] for two species, including *L. fuscula* (LeConte) = *L. nigripalpis* (LeConte), from the USA. According to RILEY et al. (2003) this genus now includes two others from the USA (*L. nitida* Wilcox and *L. semiflava* Fall). Upon close examination and comparison with many species of the genus *Varicoxa* Bechyné (1955:81) [type species: *Systena ustulata* Harold designated by BECHYNÉ (1955:81)], the author here designates *Varicoxa* Bechyné to be a synonym of *Luperaltica* Crotch. The author has examined many species of *Varicoxa* determined by Bechyné (MIZA, NHMB), including *V. ustulata* (Harold), and types of *V. ustulata centralis* Bechyné, *V. ustulata inconstans* Bechyné, as well as other reliably determined species. In the course of describing *L. nitida*, WILCOX (1953) gives a very good account of the unusual history of the species of *Luperaltica* as well as of their morphology, including aedeagus figures.

The original descriptions of both *Luperaltica* and *Varicoxa* were very inadequate. CROTCH (1873) only said that *Luperaltica* looked like *Luperus* Mueller (Galerucinae), but had "incrassate femora, entire epipleurae, separated anterior coxae ..." making it an Alticinae. Also he stated that it was similar to *Orthaltica* Crotch, but the elytra more finely sculptured, not striate, first metatarsal segment elongate, anterior coxae closed (narrowly), base of prosternum dilated to meet epimera, antennae long with basal segment short. BECHYNÉ (1955) only said that *Varicoxa* had species with closed and open procoxal cavities, heart-shaped pronotum with a weak transverse, prebasal impression, long first metatarsal segment, large head with projecting eyes wider than front margin of the pronotum. BECHYNÉ & BECHYNÉ (1967) give a checklist of the 26 described species of *Varicoxa*, 18 described by BECHYNÉ. Although the four North American species do not have the pronotum as evidently constricted basally, and *L. senilis* and *L. ni-*

gripalpis have most of the dorsum shagreened, other morphological characters, including those listed above, are the same. In addition, the males of all species have an unusually large, U-shaped opening at the apex of the strongly ventrally-projecting abdomen, apex of the aedeagus usually protruding, a thin, longitudinal, sclerotized midline on the 7th ventrite, and similar form of the aedeagus. In addition, comparing *Varicoxa ustulata*; *Luperaltica senilis*, *L. nigripalpis* in both: the metafemoral spring is identical and of the *Phyllotreta* Morpho-Group; the aedeagus is very wide in ventral/dorsal view and strongly curved in lateral view, especially in apical 1/3, very broad basal and subapical/dorsal foramina; the spermatheca is C-shaped, forming ¾ of a circle, receptacle and pump not differentiated in shape, equal width throughout, ductus a tight cluster of several coils. Therefore, the following species formerly considered as *Varicoxa* are newly combined in *Luperaltica*: *L. longicornis* (Jacoby); *L. ustulata centralis* (Bechyné); and *L. viridipennis* (Jacoby).

Changes since FURTH (2004) include:

Disonycha fumata labiata Jacoby, 1901 is synonymous with *Disonycha fumata fumata* LeConte, 1858, new synonym in BLAKE (1955: 23); *Disonycha horni* Jacoby, 1891 is synonymous with *Disonycha fumata fumata* LeConte, 1858, new synonym in BLAKE (1933b: 36).

The "Oedionychina" genera *Walterianella* Bechyné, *Alagoasa* Bechyné, and *Capraita* Bechyné are often difficult to distinguish using the traditional morphological characters as given in descriptions and keys like SCHERER (1962, 1983). There is increasing evidence that these genera and others are paraphyletic (DUCKETT & KJER 2003). *Walterianella signata* (Jacoby, 1886:431) was mistakenly listed under *Alagoasa* in FURTH & SAVINI (1996), but should have been listed as *Walterianella* as it was in WILCOX (1975), because it has the characteristics of that genus, especially the thin explanate sides of the pronotum and elytral epipleura (see SCHERER 1962, 1983); the author has examined syntypes in FCB. Also, there is increasing evidence that *Walterianella* and *Capraita* cannot reliably be separated and are possibly paraphyletic (DUCKETT & KJER 2003; C. Duckett, Washington, DC, pers. comm. 2004). The morphological characters given in SCHERER (1983), especially the prebasal, transverse impression on the pronotum, is not very reliable. However, for the present study the author prefers to retain these genera as much as possible and considers *Capraita durangoensis* (Jacoby, 1892: 318) to be best placed in the genus *Walterianella*, and as such is a new combination; the author has examined syntypes in FCB.

HORN (1889: 184) considered *Oedionychis gracilis* Jacoby as a synonym (variety) of *O. interjectionis* (Crotch 1873: 61). This was confirmed by BLAKE (1927: 15), HEIKERTINGER & CSIKI (1940), and BLACKWELDER (1946). *Oedionychis interjectionis* was apparently first considered a synonym of *Kuschelina laeta* (Perbosc 1839: 263) by WILCOX (1975) and later upheld by RILEY et al. (2003). *Kuschelina gracilis* seems to have the following morphological differences from *K. laeta*: elytra green with strongly shagreened surface, opposed to black smooth surface in *K. laeta*; longitudinal, subsutural, light stripes straight and equal in width throughout, not apically enlarged or angled outward as in *K. laeta*; pronotum distinctly punctate or shagreened, often densely, rather than smooth, mostly impunctate in *K. laeta*. There are specimens of *K. gracilis* with green elytra, without any longitudinal subsutural light stripes. The author has examined syntypes of *K. gracilis* in FCB and many specimens of *K. laeta* in USNM. Therefore, for this study the author considers *K. gracilis* and *K. laeta* to be separate and valid taxa at the species level. Further detailed study of the genitalia and molecular study may better clarify the relationship between these taxa.

FURTH & SAVINI (1996) and SAVINI & FURTH (1998) pointed out that the genus *Aphthona* Chevrolat, 1836, in its true sense from the Old World, does not exist in the New World. Most of the Neotropical species previously listed in *Aphthona* have been reassigned to *Brasilaphthona* Bechyné, 1956, *Centralaphthona* Bechyné, 1960, *Genaphthona* Bechyné, 1956. However, FURTH & SAVINI (1996) provisionally listed as *Aphthona* some Neotropical species still in need of study in order to place them in correct genera.

For *Centralaphthona* some significant characters are: convex dorsum; no pronotal transverse, subbasal impression; anterolateral angles distinctly beveled; elytra striate.

After examination of specimens determined by Jacoby (FCB) the author has determined that the following species (formerly in *Aphthona*) are best placed in *Centralaphthona* and, thus, constitute new combinations: *C. dimidiaticornis* Jacoby, 1891; *C. fulvipennis* Jacoby, 1885; *C. maculipennis* Jacoby, 1891; *C. mexicana* (Jacoby, 1885); *C. pallipes* (Jacoby, 1891); *C. semipunctata* Jacoby, 1891 [syntypes examined]; *C. substriata*, Jacoby, 1891. However, there is some indication that *Centralaphthona* Bechyné, 1960 [type species: *C. deyrollei*, Baly, 1877:296] is synonymous with *Glyptina* LeConte, 1859:26 [type species: *G. spuria* LeConte, 1859:26]. This was indicated by RILEY et al. (2002) who state that "The Neotropical genus *Centralaphthona* Bechyné, 1960, is probably a synonym [of *Glyptina* LeConte, 1859]". The author tends to agree with this statement; however, more thorough study of these genera is needed and so the above new synonyms remain as *Centralaphthona* in this study.

Aphthona pilatei Baly, *A. smithi* Jacoby, and *A. unicolor* Jacoby will tentatively remain in *Aphthona* until they can be studied further, especially type specimens. Although syntypes of *A. unicolor* (FCB) were examined by the author and it appears to belong in the "Monomacrini", further study of other genera in that putative tribe is needed.

After examination of several species determined by BECHYNÉ to be in the genus *Genaphthona*, including syntypes (FCB) of *G. transversicollis* (Jacoby), the author places *A. amulensis* Jacoby, 1891, in *Genaphthona*. This species has the flattened dorsum with very fine punctation, lateral margins of pronotum rounded, shallow subbasal, transverse pronotal impression, and very faint antennal bossae typical of *Genaphthona*.

Table 3. Mexican Alticinae by State

State	Abbreviation	No. Species
Aguascalientes	AGS	7
Baja California	BC	20
Baja California Sur	BCS	13
Campeche	CAMP	7
Chiapas	CHIS	81
Chihuahua	CHIH	43
Coahuila	COAH	11
Colima	COL	21
Distrito Federal	DF	41
Durango	DGO	97
Guanahuato	GTO	41
Guerrero	GRO	141
Hidalgo	HGO	29
Jalisco	JAL	45
Mexico	MEX	38
Michoacan	MICH	47
Morelos	MOR	84
Nayarit	NAY	23
Nuevo Leon	NL	12
Oaxaca	OAX	122
Puebla	PUE	48
Queretaro	QRO	2
Quintana Roo	QROO	8
San Luis Potosi	SLP	31
Sinaloa	SIN	17
Sonora	SON	26
Tabasco	TAB	81
Tamaulipas	TAMPS	44
Tlaxcala	TLAX	2
Veracruz	VER	198
Yucatan	YUC	23
Zacatecas	ZAC	10

Species of the genus *Gioia* Bechyné, 1955, can also be confused with *Aphthona* (SAVINI & FURTH 1996); however, *Gioia* has a very robust, convex body shape; distinctly confused and strong elytral punctures; transverse pronotum with strong punctures and thickened, broadly slanted anterolateral angles; usually evident transverse elytral impression. Considering these characters and after examining a syntype (FCB) of *A. fulvitarsis* Jacoby, 1891:246, the author concludes this species is best placed in *Gioia*.

After examination of a syntype (FCB) of *A. championi* Jacoby, 1885, and based on the characters given above, the author places this species in *Lupraea*.

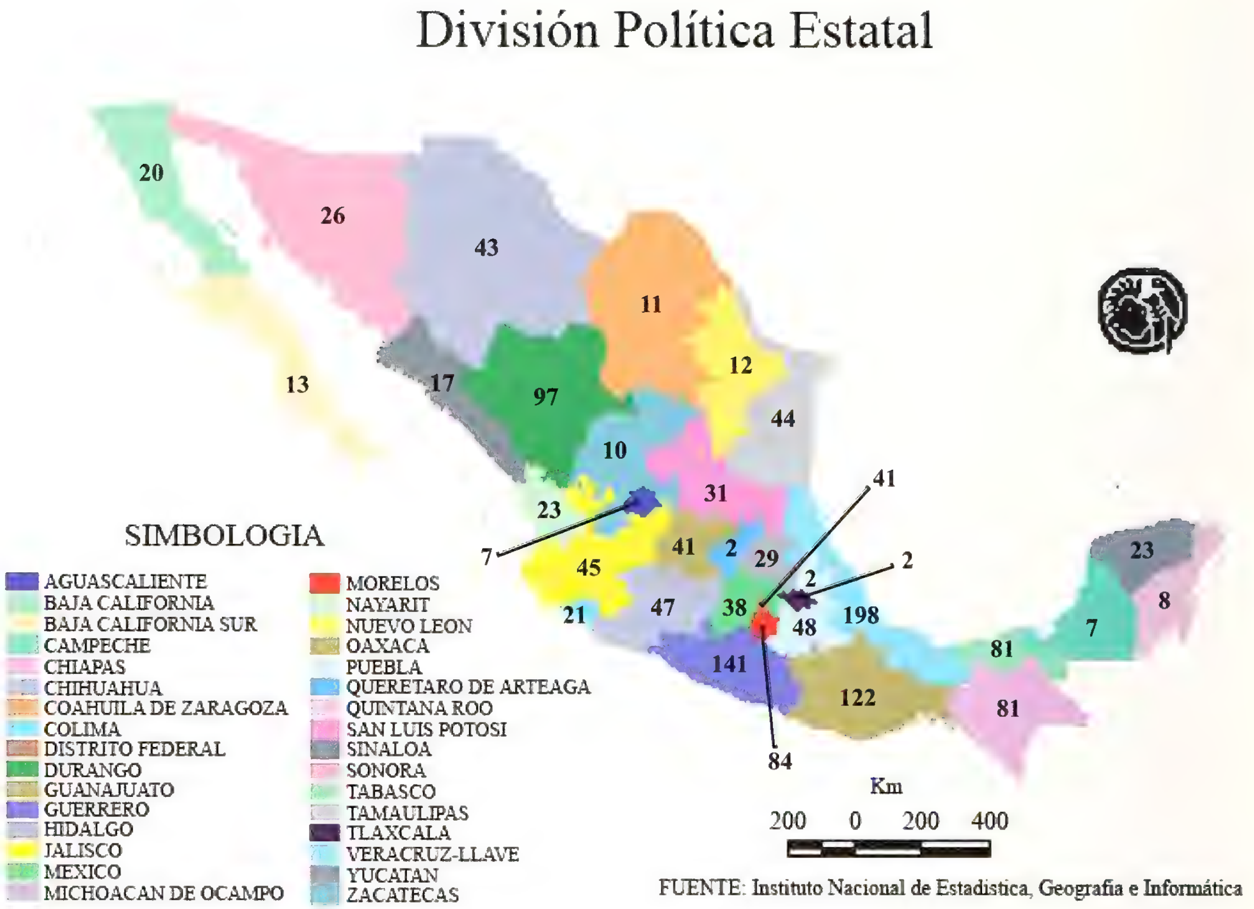
4. DISCUSSION

The author's strategy for producing an inventory or faunal list consists of three phases. First, to document the historical record through the literature. Second, to survey institutional collections; in this study including USNM, MCZC-FCB, NHMB, and ZSMC. The final phase is to conduct fieldwork. There have been very few Alticinae specialists that have collected in Mexico and none have ever lived there, so the above approach should prove very productive. Comparing the totals of genera and species recorded in the recent literature, the above-mentioned inventory method has significantly increased the totals, even at this preliminary stage. The number of recorded genera has risen from 74 to 85 (FURTH 2004), to 89, and the species from 431 to 501 (FURTH 2004) to 524. Some of the records need to be verified further, as well as some historical identifications in the FCB.

Even though this is a very preliminary list of Mexican Alticinae diversity, especially in comparison to the relatively more field-surveyed Costa Rican fauna (FURTH et al. 2003), still the Mexican fauna demonstrates high potential species richness.

Comments on Biogeography

Unlike many of the vertebrate, plant and even some insect groups mentioned above in the Introduction, species of Mexican Alticinae are poorly known. The current study is still a preliminary attempt to compile records from the literature and a few collections into a baseline from which to build in the future. Table 2 lists historical and some recently recorded (FURTH 2004) genera, including two actual newly recorded genera (*Deuteraltica* and *Heikertingeria*). Most of these genera have Neotropical affinity and in fact most are distributed deep into South America. *Gioia* was discovered recently in Mexico (SAVINI et al. 2001), but has a similar distribution to the 12 genera recorded in FURTH (2004). *Ayalaia* Bechyné & Bechyné until now was only known from El Salvador. *Deuteraltica* Bechyné & Bechyné is monotypic and previously only known from Guatemala and El Salvador. *Heikertingeria* Csiki is South American with only *H. clarki* extending into true Central America. *Luperaltica* is distinctly a Nearctic genus ex-


División Política Estatal
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SIMBOLOGIA
AGUASCALIENTE
BAJA CALIFORNIA
BAJA CALIFORNIA SUR
CAMPECHE
CHIAPAS
CHIHUAHUA
COAHUILA DE ZARAGOZA
COLIMA
DISTRITO FEDERAL
DURANGO
GUANAJUATO
GUERRERO
HIDALGO
JALISCO
MEXICO
MICHOACAN DE OCAMPO
MORELOS
NAYARIT
NUEVO LEON
OAXACA
PUEBLA
QUERETARO DE ARTEAGA
QUINTANA ROO
SAN LUIS POTOSI
SINALOA
SONORA
TABASCO
TAMAULIPAS
TLAXCALA
VERACRUZ-LLAVE
YUCATAN
ZACATECAS
Km
200 0 200 400

FUENTE: Instituto Nacional de Estadistica, Geografia e Informática

Map 1. Mexican Alticinae diversity per State

tending into the Neotropical Region. *Neothona* Bechyné is clearly a Neotropical element. *Paranaita* Bechyné is a South American genus previously only known as far north as Panama and its distribution this far north is somewhat surprising, more detailed and verification of the Mexican distribution records would be useful. *Nesaecrepida* Blake has an apparent Caribbean (Neotropical) affinity and the record in this study of the type species *N. asphaltina* in the Yucatan demonstrates the Caribbean affinities of that part of Mexico. *Exoceras* Jacoby is particularly widely distributed even throughout many Caribbean islands in almost an arc from the northern South American continent. Given the extent of the known distribution of all of the above genera it is not really surprising to find them also in Mexico. The most unusual distribution with no obvious explanation is *Terpnochlorus* Fairmaire represented in Mexico by *T. americana,* also known from Venezuela, but the genus has a very strange disjunct distribution and is also in Madagascar, central and southern Africa.

Among the other genera listed from Mexico in the Appendix the majority are of primarily Neotropical affinity. Genera such as *Altica* Geoffroy, *Chaetocnema* Stephens, *Dibolia* Latreille, *Epitrix* Foudras, *Longitarsus* Berthold, *Phyllotreta* Chevrolat, *Psylliodes* Berthold are cosmopolitan and have no particular affinity to the New World. Some genera such as *Disonycha* Chevrolat, *Kuschelina* Bechyné, *Monomacra* Chevrolat, *Systena* Chevrolat although basically Neotropical also have significant penetration at the species level into the Nearctic Region. *Crepidodera peninsularis* Horn may be a true *Crepidodera* Chevrolat in which case this is a Nearctic affinity. However, it is apparent that about 90% of the biogeographic affinity of Mexican Alticinae at the genus level is Neotropical. There are a few genera endemic to Mexico such as *Caloscelis* Clark, *Euplectroscelis* Crotch from Baja California, possibly *Iphitroides* Jacoby with four species in Mexico and one recorded species in Venezuela, but after careful study this latter species may be re-classified. A few other genera (e.g., *Dysphenges* Horn, *Phydanis* Horn, *Pseudorthygia* Csiki) were previously known only to occur in Mexico, but recently RILEY et al. (2002) recorded them occurring in extreme southern USA. A few genera are not endemic to Mexico, but most of the species in them are; e.g., *Blepharida* Chevrolat, *Chrysogramma* Jacoby, *Phyrnocepha* Baly, *Plectotetra* Baly.

Blepharida has been well studied in Mexico (Furth 1998) and there is an interesting eco-geographic pattern. New World *Blepharida* is distributed from the USA (one species) through Mexico (35 species) to Costa Rica and El Salvador (1 species). One species is also only found in the Caribbean. The genus *Notozona* Chevrolat is distributed from southern Mexico through the rest of Central America into northern South America.

Table 3 and Map 1 indicate some preliminary general trends about the diversity and biogeographic affinities of the Mexican Alticinae species. As with many other groups of animals the highest diversity is in the southern states with strong Neotropical affinities such as Chiapas, Oaxaca, Guerrero, Vera Cruz and Tabasco. The latter two demonstrate the significant Neotropical affinity that extends northward along the Caribbean coast. The rather high diversity in Durango and Morelos is not easily explainable at this time, in the Bruchidae Nápoles (2002) also recorded a high species diversity in Morelos. However, in the Alticinae possibly both the elevated numbers in Durango and Morelos as well as the relatively low number of species in the states of the Yucatan Peninsula, Aguascalientes, Queretaro, Tlaxcala, Zacatecas and others are probably primarily a factor of collecting bias; i.e., better or poorly collected areas.

Therefore, while it is more difficult to analyze the species level richness and biogeographic affinities at this very preliminary stage of knowledge of the Mexican Alticinae fauna, superficially it appears that the vast majority of species have more Neotropical affinities than Nearctic affinities.

Acknowledgements. I thank Michael Schmitt for organizing the Sixth International Symposium on the Chrysomelidae and editing its Proceedings. I am grateful to the following: E. O. Wilson and P. Perkins (MCZ, Harvard University, Cambridge) for the long-term use of the F. C. Bowditch Collection, Alexander Konstantinov (USNM, SEL, USDA) for some help with access to the collection at USNM, Santiago Niño M. (Universidad Nacional Autonoma de Tamaulipas) for specimens and records from Tamaulipas, Eva Sprecher (Naturhistorisches Museum Basel), Martin Baehr (Zoologische Staatssammlung München) and Vilma Savini (Universidad Central de Venezuela, Museo del Instituto de Zoologia Agricola, Maracay) for access to specimens at their respective museums. Support for the fieldwork by the author in Mexico (1991, 1993, 1995, 1997, 2002) was from personal funds.

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Appendix

List of genera and species names, species authors, Mexican states and the sources recorded in the literature, from the United States National Museum of Natural History (USNM) [USNM-DGF are specimens collected by the author in the USNM collection], or from the F. C. Bowditch Collection at the Museum of Comparative Zoology, Harvard University (FCB). Species names with a "?" afterwards have some question as to the correct determination of this species from Mexico. Species with a "?" after the state acronym means that there is some question as to the certainty of the locality from that state. The state acronyms are standard abbreviations for the 32 Mexican states (see Table 3). When "Mexico ?" occurs in the state column, these are records from the literature for which there is some question about the specimen being from Mexico. Sources are listed only when they represent a new or different state record. Author names for genera can be found in Furth & Savini (1996, 1998).

Genus	**Species**	**Author**	**Distribution**	**Source**
Acallepitrix	*castanea*	(Jacoby)	TAB, TAMPS, VER	Jacoby (1891)
Acallepitrix	*clypeata*	(Jacoby)	Mexico?	FCB
Acallepitrix	*fulvifrons*	(Jacoby)	GRO, MOR	FCB; Furth & Savini (1996)
Acanthonycha	*jacobyi*	Bechyné	CHIS, VER	Bechyne & Bechyne (1960); USNM
Acrocyum	*dorsalis*	Jacoby	COL, NL	Furth & Savini (1996); USNM
Acrocyum	*maculicollis*	Jacoby	DGO, MEX, VER	FCB; Jacoby (1885); USNM
Acrocyum	*sallei*	Jacoby	OAX	Jacoby (1885)
Alagoasa	*acutangula*	(Jacoby)	CHIS, COL, DGO, GRO, JAL, MEX, MOR, NL, OAX, VER	Jacoby (1886); FCB; USNM
Alagoasa	*aemulae*	(Horn)	SON	Jacoby (1892)
Alagoasa	*albomarginata*	(Latreille)	GRO	Heikertinger & Csiki (1940)
Alagoasa	*arcuatofasciata*	(Jacoby)	GRO	Jacoby (1905)
Alagoasa	*atroguttata*	(Jacoby)	COL, DGO, GRO, JAL, MOR, SLP, TAMPS, VER	Jacoby (1886); FCB; USNM
Alagoasa	*bipunctata*	(Chevrolat)	CHIS, DF, OAX, SLP, D465VER, YUC	Jacoby (1886); FCB; USNM
Alagoasa	*bipunctata boucardi*	(Harold)	VER?	NHMB
Alagoasa	*bipunctata familiaris*	(Harold)	VER?	NHMB
Alagoasa	*bipunctata salvini*	(Harold)	CHIS	NHMB
Alagoasa	*cazieri*	Pallister	CHIH	Pallister (1953)
Alagoasa	*ceracollis*	(Say)	CHIS, DGO, MOR, OAX, VER	Jacoby (1885); USNM
Alagoasa	*chevrolati*	(Baly)	OAX, VER, YUC	FCB; Furth & Savini (1996)
Alagoasa	*clypeata*	(Jacoby)	CHIS, DGO, HGO, MICH, OAX, TAB, VER	Jacoby (1892); USNM

Genus	Species	Author	Distribution	Source
Alagoasa	*decemguttatus*	(Fabricius)	CHIH, CHIS, COL, DGO, GRO, JAL, MEX, MOR, NAY, OAX, QROO, SON, TAB, VER	JACOBY (1886); FCB; PALLISTER (1953); USNM
Alagoasa	*defecta ?*	(Harold)	VER?	FCB
Alagoasa	*donckieri*	(Jacoby)	GRO	JACOBY (1905)
Alagoasa	*dugesi*	(Jacoby)	GTO	JACOBY (1886)
Alagoasa	*duodecimmaculata ?*	(Jacoby)	Mexico?	FCB
Alagoasa	*extrema*	(Harold)	MOR, OAX, TAB, VER	JACOBY (1886); FCB; USNM
Alagoasa	*fimbriata*	(Forster)	GRO, MICH, MOR, OAX	JACOBY (1886); FCB; USNM
Alagoasa	*forreri*	(Jacoby)	DGO	JACOBY (1886)
Alagoasa	*frontalis*	(Jacoby)	GRO, NAY	JACOBY (1892); NHMB
Alagoasa	*godmani*	(Jacoby)	TAB, VER	JACOBY (1886)
Alagoasa	*haroldi*	(Jacoby)	GRO, MOR, VER	JACOBY (1892)
Alagoasa	*hoegei*	(Jacoby)	OAX, VER	JACOBY (1886)
Alagoasa	*inconspicua*	(Jacoby)	DGO, JAL	JACOBY (1886); FCB
Alagoasa	*infirma*	(Jacoby)	OAX, VER	JACOBY (1886)
Alagoasa	*jalapa*	Bechyné	VER	BECHYNE (1958a)
Alagoasa	*lateralis*	(Jacoby)	COL, GRO, JAL, MEX, MICH, MOR, NAY, OAX	JACOBY (1886); FCB; USNM
Alagoasa	*longicollis*	(Jacoby)	OAX	JACOBY (1886)
Alagoasa	*millepora*	(Jacoby)	Mexico	JACOBY (1905)
Alagoasa	*pavonina*	(Jacoby)	CHIS, VER	JACOBY (1892); USNM
Alagoasa	*persimilis*	(Jacoby)	GRO	JACOBY (1905)
Alagoasa	*quadrilineata*	(Harold)	Mexico	JACOBY (1886)
Alagoasa	*semipurpurea*	(Jacoby)	VER	JACOBY (1886)
Alagoasa	*seriata*	(Baly)	GRO, MOR, OAX, PUE, VER	JACOBY (1886); FCB; NHMB
Alagoasa	*tehuacana*	Bechyné	JAL, PUE	BECHYNE (1955); USNM
Alagoasa	*tenuilineata*	(Horn)	GRO	JACOBY (1892)
Alagoasa	*tridecimmaculata*	(Jacoby)	GRO, MICH	JACOBY (1886); JACOBY (1892)
Alagoasa	*trifasciata escuintla*	Bechyné	Mexico	BECHYNE (1958a)
Alagoasa	*trilineata*	(Jacoby)	DF ?, DGO	JACOBY (1886)
Alagoasa	*violaceomarginata*	(Jacoby)	OAX	JACOBY (1886)
Alagoasa	*virgata*	(Harold)	CHIH, CHIS, COL, DGO, GRO, JAL, MEX, MOR, NAY, PUE, OAX, SIN, SLP, TAB, VER	JACOBY (1886); FCB; PALLISTER (1953); USNM; NHMB
Allochroma	*balyi*	Clark	OAX	JACOBY (1886)
Allochroma	*fasciatum*	Clark	CHIS, VER	JACOBY (1886); FCB
Allochroma	*festivus*	Clark	DGO, VER	FCB; USNM
Allochroma	*flohri*	Jacoby	Mexico	JACOBY (1892)

Genus	Species	Author	Distribution	Source
Allochroma	*fulvoplagiatum*	Jacoby	VER	Jacoby (1886)
Allochroma	*godmani*	Jacoby	OAX, VER	Jacoby (1886)
Allochroma	*guatemalensis*	Jacoby	CHIS, DGO	FCB
Allochroma	*hoegei*	Jacoby	DGO, OAX, VER	Jacoby (1886); FCB
Allochroma	*mexicanum*	Jacoby	VER	Jacoby (1886)
Allochroma	*semipunctatum*	Jacoby	OAX	Jacoby (1886)
Allochroma	*teapense*	Jacoby	TAB	Jacoby (1892)
Altica	*amicula*	(Jacoby)	DGO	Jacoby (1891)
Altica	*angulicollis*	(Jacoby)	GRO	Jacoby (1891)
Altica	*bimarginata*	(Say)	DGO, GRO, OAX, VER	FCB, Jacoby (1884)
Altica	*brisleyi*	Gentner	SON	USNM
Altica	*carinata ?*	Germar	SON ?	FCB
Altica	*complicata*	(Harold)	DF, DGO, GRO, PUE, VER	Jacoby (1884); FCB; USNM
Altica	*cupricollis*	(Jacoby)	DF, DGO, ZAC	Jacoby (1891); USNM-DGF
Altica	*flavicollis*	Jacoby	MOR	Jacoby (1884)
Altica	*foliacea*	(LeConte)	CHIH, GTO, VER	Jacoby (1891); FCB; Pallister (1953)
Altica	*forreri*	(Jacoby)	DGO, VER?	Jacoby (1884); FCB
Altica	*ignita*	(Illiger)	CHIH, BC, VER	Jacoby (1891); Pallister (1953)
Altica	*limitata*	(Jacoby)	DGO?	FCB
Altica	*litigata*	Fall	CHIS?	USNM
Altica	*marevagans ?*	Horn	CHIH, DF, SON	Jacoby (1891); FCB
Altica	*nitidiventris*	Fall	BC	Blackwelder (1946)
Altica	*obliterata*	LeConte	CHIH, SON	FCB; Jacoby (1884); Pallister (1953)
Altica	*patruelis*	Harold	DF, GRO, GTO, MEX, MICH, OAX?, PUE, TAB, VER	Jacoby (1884); FCB; USNM
Altica	*rugicollis*	Jacoby	CHIH, OAX	Jacoby (1884); FCB
Altica	*rugosa*	Jacoby	CHIH, GTO, MICH	Jacoby (1891)
Altica	*satellitia*	(Jacoby)	DGO, GRO, VER	Jacoby (1891); FCB
Altica	*schwarzi*	Blatchley	Mexico?	USNM (? Mexico, ex banana shipment)
Altica	*tincta*	LeConte	BC	Blackwelder (1946)
Altica	*tombacina*	Mannerheim	CHIH, DGO	Pallister (1953)
Altica	*torquata*	LeConte	DF, SON	Jacoby (1884); USNM
Aphthona	*pilatei*	Baly	TAB	Jacoby (1885)
Aphthona	*smithi*	Jacoby	GRO	Jacoby (1891)
Aphthona	*unicolor*	Jacoby	TAB	Jacoby (1891)
Argopistes	*rubicunda*	Blake	VER	Blake (1934)

Genus	Species	Author	Distribution	Source
Asphaera	*abdominalis*	(Chevrolat)	AGS, CHIH, CHIS, COAH, COL, DF, DGO, GRO, GTO, HGO, JAL, MEX, MICH, MOR, NL, OAX, SIN, SLP, TAMPS, VER, ZAC	JACOBY (1885 (1892)); FCB; PALLISTER (1953); USNM
Asphaera	*cyanopsis*	Harold	DF, DGO, OAX, SLP, TAB, VER	JACOBY (1885); FCB; USNM
Asphaera	*icteridera*	(Harold)	CHIS, DGO, GRO, MOR, OAX, VER	JACOBY (1885); PALLISTER (1953); USNM
Asphaera	*lustrans*	(Crotch)	BC	BLACKWELDER (1946)
Asphaera	*mexicana*	(Harold)	CHIS, DGO, GRO, MICH, MOR, NAY, OAX, VER	JACOBY (1886); FCB; USNM
Asphaera	*nigrofasciata*	Jacoby	VER	USNM
Asphaera	*nobilitata*	(Fabricius)	CHIS	USNM
Asphaera	*polita*	Jacoby	OAX, TAB, VER	JACOBY (1885); FCB
Asphaera	*reichei*	(Harold)	CHIS, DF, OAX, SLP, VER	JACOBY (1885); USNM
Asphaera	*xanthocephala*	Harold	VER	FURTH & SAVINI (1996)
Ayalaia	*minor*	Bechyné & Bechyné	GRO?, NAY	USNM
Blepharida	*alternata*	Jacoby	CHIS, GRO, JAL, MOR, NAY, SLP, SIN, SON	FURTH (1998)
Blepharida	*alticola*	Achard	CHIS, DGO	FURTH (1998)
Blepharida	*atripennis*	Horn	BCS	FURTH (1998)
Blepharida	*balyi*	Bryant	GRO, MEX, MICH, MOR	FURTH (1998)
Blepharida	*bryanti*	Furth	CHIS, OAX	FURTH (1998)
Blepharida	*conspersa*	(Horn)	BCS	FURTH (1998)
Blepharida	*flavocostata*	Jacoby	GRO, MEX, MICH, MOR, OAX, PUE	FURTH (1998)
Blepharida	*flohri*	Jacoby	GRO, JAL, MEX, MICH, MOR, NAY	FURTH (1998)
Blepharida	*gabrielae*	Furth	COL, GRO, JAL, MEX, MICH. MOR, PUE	FURTH (1998)
Blepharida	*godmani*	Jacoby	CHIS, OAX, VER	FURTH (1998)
Blepharida	*hinchahuevosi*	Furth	GRO, MOR, PUE	FURTH (1998)
Blepharida	*humeralis*	Furth	GRO, MOR, PUE	FURTH (1998)
Blepharida	*jacobyana*	Csiki	CHIS, QROO, VER, YUC	FURTH (1998)
Blepharida	*johngi*	Furth	DGO, GRO, MEX, MICH	FURTH (1998)
Blepharida	*judithae*	Furth	GRO	FURTH (1998)

Genus	Species	Author	Distribution	Source
Blepharida	*lineata*	Furth	GRO, MICH	Furth (1998)
Blepharida	*maculicollis*	Jacoby	MOR, PUE	Furth (1998)
Blepharida	*melanoptera*	(Fall)	MICH, OAX, SON	Furth (1998)
Blepharida	*mexicana*	Jacoby	OAX, VER	Furth (1998)
Blepharida	*multimaculata*	Jacoby	GRO, MEX, MOR, PUE, SON	Furth (1998)
Blepharida	*notozonae*	Furth	JAL, SIN, SON	Furth (1998)
Blepharida	*pallida*	Blake	GRO, JAL, MICH, SIN	Furth (1998)
Blepharida	*parallela*	Furth	MEX, MICH, PUE	Furth (1998)
Blepharida	*punctatissima*	Jacoby	CHIS, OAX, VER	Furth (1998)
Blepharida	*quatuordecimpunctata*	Jacoby	CHIS, OAX, VER	Furth (1998)
Blepharida	*rhois*	(Forster)	CHIH, COAH, DGO, GRO, HGO, NL, OAX, PUE, QRO, SLP, TAMPS	Furth (1998)
Blepharida	*schlectendalii*	Furth	PUE	Furth (1998)
Blepharida	*singularis*	Jacoby	DGO, GRO, MEX, MICH, MOR, PUE	Furth (1998)
Blepharida	*sonorana*	Furth	SIN, SON	Furth (1998)
Blepharida	*sonorstriata*	Furth	SON	Furth (1998)
Blepharida	*sparsa*	(Clark)	CHIS, GRO, MICH	Furth (1998)
Blepharida	*trifasciata*	Jacoby	OAX	Furth (1998)
Blepharida	*unami*	Furth	OAX, PUE	Furth (1998)
Blepharida	*variegatus*	Furth	PUE	Furth (1998)
Blepharida	*verdea*	Furth	GRO, MOR, OAX	Furth (1998)
Blepharida	*xochipala*	Furth	GRO	Furth (1998)
Cacoscelis	*bicolorata*	Clark	Mexico	Jacoby (1884)
Cacoscelis	*coerulea*	Csiki	TAB	Jacoby (1892)
Cacoscelis	*flava*	Clark	OAX, TAMPS	Jacoby (1884); USNM
Cacoscelis	*sallei*	Jacoby	VER	Jacoby (1884)
Cacoscelis	*varians*	(Jacoby)	OAX, TAB, VER	Jacoby (1891)
Caloscelis	*nigripennis*	(Jacoby)	NAY	Jacoby (1891)
Capraita	*conspurcata*	(Jacoby)	CHIS, DF, DGO, GRO, GTO, HGO, MEX, MICH, MOR, OAX, PUE, VER	Jacoby (1886); FCB; USNM
Capraita	*maculata*	(Harold)	CHIS, GRO, JAL, MEX, MOR, OAX, VER, YUC	Jacoby (1886); FCB
Capraita	*maculata tredecimmaculata*	(Jacoby)	GRO, HGO, MEX	USNM; NHMB
Capraita	*nigrosignata*	(Schaeffer)	Mexico ?	USNM (? Mexico, ex snapdragon shipment)
Centralaphthona	*deyrollei*	(Baly)	JAL, MOR, TAB	Jacoby (1885): USNM
Centralaphthona	*dimidiaticornis*	Jacoby	GRO, TAB	Jacoby (1891); FCB

Genus	Species	Author	Distribution	Source
Centralaphthona	*diversa*	(Baly)	CHIS, GRO, MOR, TAB, TAMPS?	JACOBY (1885); FCB; USNM
Centralaphthona	*fulvipennis ?*	Jacoby	VER?	FCB
Centralaphthona	*fulvipennis near*	Jacoby	TAMPS	USNM-El Cielo
Centralaphthona	*maculipennis*	Jacoby	TAB	JACOBY (1891)
Centralaphthona	*mexicana*	Jacoby	COAH, DGO, GRO	JACOBY (1885) (1891); FCB
Centralaphthona	*obscuripennis*	(Jacoby)	GRO, MOR	USNM
Centralaphthona	*pallipes*	Jacoby	CHIH, GRO, VER	JACOBY (1891); USNM-DGF
Centralaphthona	*semicoerulea*	(Jacoby)	DGO	JACOBY (1885)
Centralaphthona	*semipuncata*	Jacoby	JAL, VER	JACOBY (1891); FCB
Centralaphthona	*substriata*	Harold	GRO, TAB, VER	JACOBY (1891)
Chaetocnema	*balyi*	Jacoby	COAH, DF	JACOBY (1892); FCB
Chaetocnema	*capitata*	Jacoby	DGO, GTO	JACOBY (1885); FCB
Chaetocnema	*cephalotes*	Jacoby	PUE, SIN	NHMB
Chaetocnema	*confinis*	Crotch	DF	USNM
Chaetocnema	*costatipennis*	Jacoby	GTO	JACOBY (1892)
Chaetocnema	*cribrifrons*	LeConte	CHIH, DGO	PALLISTER (1953)
Chaetocnema	*discoidalis*	Jacoby	Mexico	JACOBY (1885)
Chaetocnema	*ectypa*	Horn	CHIH ?	USNM (ex mustard shipment from Juarez)
Chaetocnema	*frontalis ?*	Jacoby	Mexico	FCB
Chaetocnema	*fulvicornis*	Jacoby	DGO, GRO, GTO	JACOBY (1885); FCB
Chaetocnema	*fulvida*	White	BCS	USNM
Chaetocnema	*fulvilabris*	Jacoby	GRO, MOR, VER	JACOBY (1892); USNM
Chaetocnema	*gravida*	Baly	JAL, TAB	JACOBY (1885): FCB
Chaetocnema	*horni*	Jacoby	TAB	JACOBY (1892)
Chaetocnema	*interstitialis*	Jacoby	GRO	JACOBY (1892)
Chaetocnema	*mexicana*	Baly	CAMP, COAH, DF, DGO, MOR, TAB	JACOBY (1885); FCB; USNM
Chaetocnema	*parcepunctata*	Crotch	DF	JACOBY (1892)
Chaetocnema	*sallei*	Baly	Mexico	JACOBY (1885)
Chaetocnema	*smithi*	Jacoby	TAB	JACOBY (1892)
Chalatenanganya	*frontalis*	(Jacoby)	CHIS	NEW – DGF; USNM
Chrysogramma	*octomaculata*	Jacoby	CHIS, JAL, VER	DOMINGUEZ & CARRILLO (1976); USNM
Chrysogramma	*omiltenaia*	Jacoby	GRO	JACOBY (1891)
Chrysogramma	*pictipennis*	Jacoby	DGO	JACOBY (1891)
Chrysogramma	*septempunctata*	Jacoby	DGO, MOR, OAX, PUE	USNM; FURTH & SAVINI (1996)
Chrysogramma	*trifasciata*	Jacoby	OAX	JACOBY (1891)
Cornulactica	*varicornis*	(Jacoby)	VER	JACOBY (1891)
Crepidodera	*opulenta ?*	(LeConte)	BC, MOR	USNM

Genus	Species	Author	Distribution	Source
Crepidodera	*peninsularis*	Horn	BC	Furth & Savini (1998)
Cyrsylus	*fulvipes*	Jacoby	TAB	Jacoby (1892)
Cyrsylus	*recticollis*	Jacoby	CHIS, TAB, VER	Jacoby (1892); USNM
Cyrsylus	*vittatus*	Jacoby	CHIS, GRO, GTO, JAL	Jacoby (1892); USNM
Deuteraltica	*longicornis*	(Jacoby)	CHIS	USNM
Dibolia	*championi*	Jacoby	OAX, VER	Parry (1974); USNM
Dibolia	*constricta*	Jacoby	DGO, VER	Jacoby (1891)
Dibolia	*ovata*	LeConte	DF, DGO, GRO, GTO, MICH, VER	Jacoby (1891); FCB; USNM
Dibolia	*violacea*	Jacoby	GRO	Jacoby (1891)
Dinaltica	*chevrolati*	(Jacoby)	VER	Jacoby (1884)
Diphaltica	*chiriquiensis ?*	(Jacoby)	VER	FCB; USNM
Diphaltica	*columbica*	(Harold)	VER	Jacoby (1884)
Diphaltica	*crassicornis ?*	(Jacoby)	TAB, VER	FCB
Diphaltica	*fossifrons*	(Harold)	VER	Jacoby (1891)
Diphaltica	*nitida*	(Jacoby)	CHIS, DF, DGO, MICH, OAX, TAB, VER	Jacoby (1884); FCB; USNM
Diphaltica	*panamensis ?*	(Jacoby)	DGO	FCB
Diphaltica	*sallei*	(Harold)	Mexico	Harold (1876)
Diphaltica	*sobrina*	Jacoby	VER	Jacoby (1884)
Diphaulaca	*aulica cordobae*	Barber	CHIS, GRO, GTO, HGO, JAL, MEX, MICH, MOR, NAY, OAX, PUE, QROO, SLP?, TAB, TAMPS, VER, YUC	Jacoby (1884); FCB; USNM
Diphaulaca	*intermedia*	Jacoby	GRO	Jacoby (1891)
Diphaulaca	*wagneri*	Harold	CHIS, GRO, OAX, YUC	Barber (1941); NHMB
Disonycha	*discoidea abbreviata*	Melsheimer	DGO, MEX, MOR, OAX	Jacoby (1884); FCB
Disonycha	*angulata*	Jacoby	SLP, TAB, VER, YUC	Jacoby (1891)
Disonycha	*annulata*	Blake	Mexico	Blake (1955)
Disonycha	*antennata*	Jacoby	COL, DGO, GRO, JAL, MEX, MICH, MOR, OAX, VER	Jacoby (1884); Blake (1955); USNM
Disonycha	*apicalis*	Jacoby	VER	Jacoby (1884)
Disonycha	*arizonae*	Casey	CHIH, DGO?, GRO, MOR?	Furth & Savini (1996); USNM
Disonycha	*barberi*	Blake	GRO, SIN, VER	Blake (1955); USNM
Disonycha	*brevicollis*	Jacoby	DGO	Jacoby (1902)
Disonycha	*brevilineata*	Jacoby	DGO, GRO, JAL, MOR, OAX	Jacoby (1884); Jacoby (1902); FCB; Blake (1955)

Genus	**Species**	**Author**	**Distribution**	**Source**
Disonycha	*brunneofasciata*	Jacoby	GRO, PUE, SLP	Blake (1955); USNM
Disonycha	*caroliniana*	(Fabricius)	DGO, NL, OAX, SIN, VER	Jacoby (1884); USNM
Disonycha	*collata*	(Fabricius)	CHIH, COAH, DF, DGO, GTO, JAL, MEX, MICH, MOR, OAX, PUE, TAB, VER, YUC	Jacoby (1884); FCB; Pallister (1953); USNM
Disonycha	*crenicollis*	Say	PUE, SON	Jacoby (1884)
Disonycha	*dorsata*	Harold	MOR, OAX, TAB, VER, YUC	Jacoby (1884); FCB; USNM
Disonycha	*figurata*	Jacoby	AGS, CHIH, CHIS, COAH, COL, DF, DGO, GRO, GTO, JAL, MEX, MICH, MOR, NAY, OAX, SIN, TAB, VER, YUC	Jacoby (1884); FCB; Pallister (1953); Blake (1955); USNM; NHMB
Disonycha	*fumata fumata*	LeConte	BC, CHIH, CHIS, DGO, GRO, HGO, JAL, MEX, MICH, MOR, NL, OAX, PUE, SLP, SON, TAB, VER, ZAC	Blake (1955); USNM
Disonycha	*fumata quinquerutata*	Schaeffer	CHIH	Pallister (1953)
Disonycha	*glabrata*	(Fabricius)	BC, BCS, CAMP, CHIS, COL, DGO, GRO, JAL, MOR, NAY, OAX, PUE, SIN, SON, TAB, TAMPS, YUC, VER	Jacoby (1884); FCB; Blake (1955); USNM
Disonycha	*gracilis*	Blake	VER	Blake (1955)
Disonycha	*guatemalensis*	Jacoby	CHIS, GRO, MOR, OAX, VER?	Blake (1955); USNM
Disonycha	*hoegei*	Jacoby	VER, OAX	Jacoby (1884)
Disonycha	*jalapensis*	Blake	VER	Blake (1955)
Disonycha	*knabi*	Blake	GRO	Blake (1955)
Disonycha	*latifrons*	Schaeffer	TAMPS?	USNM
Disonycha	*latiovittata*	Hatch & Beller	BC	Blake (1955)
Disonycha	*leptolineata texana*	Schaeffer	DGO, GRO, JAL, MOR, NL, OAX, QROO, TAMPS, YUC	Blake (1955); USNM
Disonycha	*limbata*	Jacoby	DGO, MEX, MOR	Jacoby (1891); USNM
Disonycha	*maculipes*	Jacoby	CHIS, VER	Jacoby (1891); USNM
Disonycha	*melanocephala*	Jacoby	VER	Jacoby (1884)

Genus	Species	Author	Distribution	Source
Disonycha	*mexicana*	Jacoby	TAB, SLP, VER, YUC	FCB; JACOBY (1884)
Disonycha	*militaris*	Jacoby	TAB, VER, YUC	JACOBY (1884); USNM
Disonycha	*nigripennis*	Jacoby	DGO, NAY	JACOBY (1884); USNM
Disonycha	*nigripes ?*	Jacoby	CHIS	FCB
Disonycha	*pluriligata*	LeConte	BC, CHIH, DGO, JAL, NAY, SIN, SLP, SON, VER	FCB; FURTH & SAVINI (1996)
Disonycha	*politula*	Horn	AGS, CAMP, CHIH, DF, DGO, GRO, GTO, HGO, JAL, MEX, MOR, OAX, PUE, QRO, SLP, SON, TAMPS, VER, ZAC	FCB; JACOBY (1891); PALLISTER (1953); USNM
Disonycha	*procera*	Casey	NAY	BLAKE (1955)
Disonycha	*quinquelineata*	(Latreille)	CHIS, COL, GRO, OAX, QROO, TAB, TAMPS, VER	JACOBY (1884); FCB; BLAKE (1955); USNM
Disonycha	*recticollis*	(Jacoby)	NAY, VER	JACOBY (1884); ZSMC
Disonycha	*sallei*	(Baly)	VER	JACOBY (1884)
Disonycha	*scriptipennis*	(Jacoby)	CHIS, COL, DGO, GRO, MOR, NAY, OAX, YUC	JACOBY (1891); USNM; NHMB
Disonycha	*steinheili*	Harold	Mexico	ZSMC
Disonycha	*subaenea*	Jacoby	DGO, GRO, MOR, OAX	JACOBY (1884); FCB; USNM
Disonycha	*subcostata*	(Clark)	HGO, MEX, MICH	JACOBY (1884); USNM
Disonycha	*teapensis*	Blake	OAX, SLP, TAB	BLAKE (1955); NHMB
Disonycha	*tenuicornis*	Horn	CHIH, DGO, HGO	PALLISTER (1953); BLAKE (1955)
Disonycha	*trifasciata*	Jacoby	CHIS	FCB
Disonycha	*trivittata*	Blake	Mexico	BLAKE (1955)
Disonycha	*varicornis*	Horn	BC, BCS, DGO, TAMPS	FURTH & SAVINI (1998); PALLISTER (1953); USNM
Distigmoptera	*chrysodaedala*	Blake	DF, NAY	BLAKE (1951); USNM
Distigmoptera	*foveolata*	Balsbaugh	CHIS, PUE	BALSBAUGH (1980); USNM
Distigmoptera	*orchidophila*	Blake	VER	BLAKE (1951)
Distigmoptera	*suturalis*	(Jacoby)	GRO, OAX	JACOBY (1892); NHMB

Genus	**Species**	**Author**	**Distribution**	**Source**
Distigmoptera	*texana*	Blake	GTO	BLASBAUGH (1980); FURTH & SAVINI (1998)
Dysphenges	*eichlini*	Gilbert & Andrews	BCS	GILBERT & ANDREWS (2002)
Dysphenges	*elongatulus*	Horn	BCS, MICH?, PUE?, TAMPS?	GILBERT & ANDREWS (2002); USNM
Dysphenges	*lagunae*	Gilbert & Andrews	BCS	GILBERT & ANDREWS (2002)
Dysphenges	*rileyi*	Gilbert & Andrews	BCS	GILBERT & ANDREWS (2002)
Egleraltica	sp.		CHIS, GRO, MICH, MOR	USNM
Epitrix	*aenicollis*	Jacoby	GRO, TAB, VER	JACOBY (1891)
Epitrix	*convexa*	Jacoby	TAB, VER	JACOBY (1891)
Epitrix	*cucumeris*	(Harris)	DGO, GRO, MOR, PUE, VER	JACOBY (1891); FCB; USNM; ZSMC
Epitrix	*fasciata*	Blatchley	CHIH, DGO, NL, TAMPS	MAES & STAINES (1991); USNM
Epitrix	*flavotestacea*	Horn	BC	BLACKWELDER (1946)
Epitrix	*fuscula*	Crotch	GTO?	JACOBY (1885)
Epitrix	*jacobyi*	Weise	GTO, VER	JACOBY (1885)
Epitrix	*metallica*	Jacoby	GRO	JACOBY (1885)
Epitrix	*minuta*	Jacoby	VER, TAB	FCB, JACOBY (1891)
Epitrix	*montana*	Jacoby	VER, COAH	JACOBY (1885)
Epitrix	*nigroaenea*	Harold	VER	JACOBY (1885)
Epitrix	*obliterata*	Jacoby	TAB, VER	JACOBY (1891); FCB
Epitrix	*parvula*	(Fabricius)	CHIH, GTO, VER	FCB, JACOBY (1891); USNM-DGF
Epitrix	*piceomarginata*	Jacoby	TAB	JACOBY (1891)
Epitrix	*pulchella*	Jacoby	TAB, VER	FCB, JACOBY (1885)
Epitrix	*robusta*	Jacoby	GRO	JACOBY (1891)
Epitrix	*rufula*	Weise	DF, GRO, MOR	JACOBY (1891); USNM
Euphenges	*fulginosus*	(Clark)	Mexico	JACOBY (1886)
Euplectroscelis	*xanti*	Crotch	BC; BCS	BLACKWELDER (1946); USNM
Exoceras	sp.		CHIS	USNM
Genaphthona	*amulensis*	Jacoby	GRO	JACOBY (1891)
Genaphthona	*transversicollis*	(Jacoby)	CHIS, JAL, OAX, PUE	USNM
Gioia	*fulvitarsis*	Jacoby	TAB	JACOBY (1891)
Gioia	*mexicana*	Savini, Furth, Nino	TAMPS	SAVINI et al. (2001)
Gioia	sp. 1		TAMPS	SAVINI et al. (2001)
Gioia	sp. 2		TAMPS	SAVINI et al. (2001)

Genus	Species	Author	Distribution	Source
Glenidion	*flexicaulis*	Schaeffer	TAMPS, YUC	USNM
Glenidion	*jacobyi*	(Bechyné)	CHIS, MICH, VER	Jacoby (1885); USNM
Glyptina	*atriventris*	Horn	CHIH, MICH	USNM
Glyptina	*cerina*	(LeConte)	BC	Blackwelder (1946)
Glyptina	*nivialis*	Horn	MOR	USNM
Heikertingerella	*fulvifrons*	(Jacoby)	GRO, VER	Jacoby (1891)
Heikertingerella	*pallida*	Jacoby	VER	Jacoby (1891)
Heikertingerella	*teapensis*	(Weise)	TAB	Jacoby (1892)
Heikertingerella	*variabilis*	(Jacoby)	GRO, GTO, TAB, TAMPS, VER	Jacoby (1885); FCB; USNM
Heikertingeria	*clarki*	(Jacoby)	VER	USNM
Hemiphyrnus	*intermedius*	(Jacoby)	CHIS, DGO, SON	FCB, Jacoby (1884)
Homotyphus	*asper*	(Clark)	VER	Jacoby (1886)
Homotyphus	*maculicornis*	(Clark)	VER	USNM; Furth & Savini (1996)
Homotyphus	*squalidus ?*	Clark	VER	Jacoby (1886)
Hypolampsis	*elongatula*	(Jacoby)	GRO	Jacoby (1892)
Hypolampsis	*inornata*	Jacoby	GRO	Jacoby (1892)
Hypolampsis	*labialis*	(Clark)	VER	Jacoby (1886)
Hypolampsis	*pygmaea*	(Jacoby)	TAB, VER	Jacoby (1892)
Iphitroides	*nigrocinctus*	Jacoby	GRO	Jacoby (1891)
Iphitroides	*quadrimaculatus*	Jacoby	DGO, GRO	Jacoby (1891): USNM
Iphitroides	*quadripunctatus*	Jacoby	GRO, MOR, NAY	Jacoby (1891); USNM
Iphitroides	*violaceipennis*	Jacoby	Mexico?	Jacoby (1891)
Kuschelina	*gracilis*	(Jacoby)	COL, JAL, MOR, SIN	USNM; NHMB
Kuschelina	*laeta*	(Perbosc)	TAMPS, VER	Heikertinger & Csiki (1940); FCB; USNM
Kuschelina	*lugens*	(LeConte)	Mexico?	USNM
Kuschelina	*miniata ?*	(Fabricius)	Mexico	FCB
Kuschelina	*modesta*	(Jacoby)	CHIH, CHIS, DF, DGO, GRO, GTO, HGO, MEX, MOR, OAX, PUE, SLP, TLAX, VER	Jacoby (1886); FCB; Pallister (1953); USNM
Kuschelina	*petaurista ?*	(Fabricius)	COAH	USNM
Kuschelina	*violascens*	(LeConte)	DGO	Furth & Savini (1998); Pallister (1953)
Leptophysa	*hirtipennis*	(Jacoby)	OAX, VER	USNM
Longitarsus	*amulensis*	Jacoby	GRO	Jacoby (1891)
Longitarsus	*antennatus*	Jacoby	VER	Jacoby (1891)
Longitarsus	*bicolor*	Horn	BC	Blackwelder (1946); Furth & Savini (1998)
Longitarsus	*buckleyi ?*	Baly	TAB	FCB

Genus	Species	Author	Distribution	Source
Longitarsus	*columbicus ?*	Harold	GRO	FCB
Longitarsus	*concinnus*	Baly	Mexico?	Jacoby (1885)
Longitarsus	*haroldi*	Jacoby	TAB	Jacoby (1891)
Longitarsus	*livens*	LeConte	BC	Blackwelder (1946)
Longitarsus	*mexicanus*	Csiki	DF, DGO, GRO, GTO, HGO, MEX, MICH, MOR, PUE	Jacoby (1891); FCB; NHMB; USNM
Longitarsus	*ovipennis*	Jacoby	GRO	Jacoby (1891)
Longitarsus	*repandus*	LeConte	BC	Blackwelder (1946)
Longitarsus	*teapensis*	Jacoby	TAB	Jacoby (1891)
Longitarsus	*varicornis*	Suffrian	TAB, VER	Jacoby (1885); Jacoby (1891)
Luperaltica	*longicornis*	(Jacoby)	CHIS, COL?, MOR?, OAX?	USNM
Luperaltica	*ustulata centralis*	(Bechyné)+C254	NAY, TAMPS	Bechyne (1960); USNM
Luperaltica	*viridipennis*	(Jacoby)	OAX	Jacoby (1884)
Lupraea	*championi*	Jacoby	VER	Jacoby (1885)
Lupraea	*dilaticornis*	(Jacoby)	VER	Jacoby (1891)
Lupraea	*elongata*	(Jacoby)	GRO, MICH	USNM
Lupraea	*frontalis*	(Jacoby)	OAX	Jacoby (1885); USNM
Lupraea	*fulvicollis ?*	Jacoby	VER	FCB
Lupraea	*godmani*	(Jacoby)	TAB, VER?	Jacoby (1891); USNM
Lupraea	*guatemalensis*	(Jacoby)	CHIS, GRO, MOR, VER	Jacoby (1891); USNM
Lupraea	*imitans*	(Jacoby)	GRO, VER?	Jacoby (1891); USNM
Lupraea	*occipitalis*	Bechyné & Bechyné	Mexico?	Bechyne & Bechyne (1964)
Lupraea	*semifulva*	(Jacoby)	CHIS, OAX	USNM-DGF
Lupraea	*smithi*	(Jacoby)	GRO, MOR	Jacoby (1891); USNM-DGF
Lysathia	*jacobyi*	(Csiki)	DF, GTO, OAX, TAB, ZAC	Jacoby (1891); USNM
Lysathia	*ludoviciana*	(Fall)	Mexico?	USNM (on banana; Galveston)
Lysathia	*occidentalis*	(Suffrian)	YUC	ZSMC
Lysathia	*rockefelleri*	(Pallister)	CHIH, DGO	Pallister (1953)
Macrohaltica	*amethystina*	(Olivier)	PUE, VER	Jacoby (1884)
Macrohaltica	*guatemalensis*	(Jacoby)	DF, GRO, SON	Jacoby (1891); Furth & Savini (1998); USNM
Macrohaltica	*jamaicensis*	(Fabricius)	TAMPS	USNM
Macrohaltica	*mexicana mexicana*	(Jacoby)	DF, DGO, MOR	Jacoby (1884); FCB; USNM
Macrohaltica	*mexicana salvadorensis*	Bechyné	CHIS, DF, DGO	USNM

Genus	Species	Author	Distribution	Source
Macrohaltica	*patruelis*	(Harold)	DF, DGO, GTO, MEX, MICH, MOR, OAX, PUE, VER	Jacoby (1884); USNM
Margaridisa	*atriventris*	(Melsheimer)	CHIS, VER	USNM
Margaridisa	*managua ?*	(Bechyné)	DGO, SLP	USNM
Mesodera	*brevicollis*	Jacoby	HGO	Jacoby (1892)
Monomacra	*abdominalis*	(Jacoby)	CAMP, YUC	USNM
Monomacra	*binotata*	(Baly)	TAB, VER	Jacoby (1884); USNM
Monomacra	*crassicornis*	(Jacoby)	CHIS, GRO	Jacoby (1891)
Monomacra	*cupreata*	(Jacoby)	OAX	Jacoby (1891)
Monomacra	*elongata*	(Jacoby)	DGO	Jacoby (1884)
Monomacra	*gracilicornis*	(Jacoby)	Mexico	Jacoby (1902)
Monomacra	*hidalgoensis*	(Jacoby)	HGO	Jacoby (1892)
Monomacra	*hoegei*	(Jacoby)	OAX, VER	Jacoby (1884)
Monomacra	*inornata ?*	(Jacoby)	Mexico	FCB
Monomacra	*mexicana*	(Jacoby)	OAX, VER	Jacoby (1884); USNM
Monomacra	*nicotinae*	(Jacoby)	TAMPS, VER	Jacoby (1904); USNM
Monomacra	*pusilla*	(Jacoby)	VER	Jacoby (1884)
Monomacra	*salvini*	(Jacoby)	CHIH	FCB
Monomacra	*semiviolacea*	(Jacoby)	TAMPS	Jacoby (1884); USNM
Monomacra	*tibialis*	(Olivier)	OAX	USNM
Monomacra	*violacea*	(Jacoby)	CHIS, VER	USNM-DGF
Monomacra	*violaceipennis*	(Jacoby)	Mexico ?	Jacoby (1884)
Neodiphaulaca	*elongatula*	(Harold)	DGO, SLP, VER	Heikertinger & Csiki (1939), FCB; USNM
Neothona	sp.		JAL, MICH, OAX, VER	USNM
Nesaecrepida	*infuscata*	(Schaeffer)	CAMP, COL, GRO, JAL, MICH, OAX, TAB, TAMPS, VER	USNM; USNM-DGF; ZSMC
Nesaecrepida	*asphaltina*	(Suffrian)	YUC	USNM
Notozona	*elegans*	Clark	Mexico	Jacoby (1885)
Notozona	*histrionica*	Baly	OAX, VER	FCB; Furth & Savini (1996)
Notozona	*humilis*	Clark	Mexico	Jacoby (1885)
Omophoita	*aequatorialis*	(Harold)	Mexico	Jacoby (1885)
Omophoita	*aequinoctialis aequinoctialis*	(Linnaeus)	CHIS, HGO, MICH, OAX, QROO, SLP, TAB, TAMPS, VER	Furth & Savini (1996); USNM
Omophoita	*albofasciata*	(Jacoby)	TAB	FCB
Omophoita	*affinis ?*	(Jacoby)	Mexico ?	FCB
Omophoita	*championi*	(Jacoby)	SON	Dominguez & Carrillo (1976)
Omophoita	*cinctipennis*	(Chevrolat)	JAL, OAX, PUE, SLP, VER	Jacoby (1885); USNM

Genus	**Species**	**Author**	**Distribution**	**Source**
Omophoita	*clerica*	(Erichson)	CHIS	USNM
Omophoita	*octomaculata*	(Crotch)	OAX, TAB, TAMPS, VER	Jacoby (1886); ZSMC
Omophoita	*punctulata*	(Bechyné & Bechyné)	Mexico	Bechyne & Bechyne (1963)
Omophoita	*quadrinotata centraliamericana*	Bechyné	OAX, TAB, VER	Bechyne (1955); USNM
Omophoita	*recticollis*	(Baly)	CHIS, HGO, OAX, TAB, TAMPS, VER	Jacoby (1885) (1891); USNM
Omophoita	*simulans*	(Jacoby)	CHIS, DGO	Jacoby (1892)
Omophoita	*violacea*	Jacoby	GRO	Jacoby (1892)
Palaeothona	*discrepans*	(Schaeffer)	CHIH	USNM-DGF
Palaeothona	*melanocyanea*	(Blake)	HGO, TAMPS	Blake (1950); Furth & Savini (1998); USNM
Palaeothona	*rubroviridis*	Blake	DGO	Blake (1950)
Palaeothona	*rugifrons*	(Jacoby)	VER	Jacoby (1885)
Palaeothona	*viridis (near)*	(Jacoby)	CHIH	NEW – DGF (PDST)
Paranaita	*limbatipennis*	(Jacoby)	GRO?	ZSMC
Parasyphraea	*minuta*	(Jacoby)	TAB, YUC	Jacoby (1891); USNM
Parchicola	*uniformis ?*	(Jacoby)	Mexico	FCB
Parchicola	*variabilis*	(Jacoby)	CHIS, VER	Jacoby (1884); USNM
Pedilia	*inornata*	(Jacoby)	OAX, VER	Duckett (1993) in litt.
Phenrica	*cordovana*	(Jacoby)	VER	Jacoby (1884)
Phenrica	*sexmaculata*	(Jacoby)	VER	Jacoby (1884)
Phrynocepha	*capitata*	Jacoby	CHIS?, GRO, JAL, OAX, TAB?	Jacoby (1884); USNM
Phrynocepha	*deyrollei*	Baly	AGS, CHIH, DGO, GRO, GTO, MICH, MOR, OAX, PUE, SLP ?	Jacoby (1884); Pallister (1953); USNM
Phrynocepha	*elongata*	Jacoby	OAX, TLAX, VER	Jacoby (1884)
Phrynocepha	*pulchella*	Baly	CHIS, COL, DGO, GTO, JAL, MICH, MOR, OAX, VER	Jacoby (1884); USNM; NHMB
Phrynocepha	*punctulata*	Pallister	CHIH, DGO	Pallister (1953)
Phrynocepha	*sulcatipennis*	(Jacoby)	GRO, MEX, OAX	Jacoby (1891); NHMB
Phrynocepha	*tenuicornis*	(Jacoby)	HGO, OAX	FCB; Jacoby (1891)
Phydanis	*bicolor*	Horn	OAX, TAMPS	USNM
Phydanis	*nigriventris*	Jacoby	GRO, OAX, SLP, SON	Jacoby (1891); USNM
Phyllotreta	*albionica*	(LeConte)	BC, CHIH, SON	Fall (1927); Furth & Savini (1998); USNM

Genus	Species	Author	Distribution	Source
Phyllotreta	*crotchi*	Jacoby	DF, DGO, HGO, MEX, ZAC	Jacoby (1885) (1891); USNM
Phyllotreta	*lativittata*	Jacoby	DF, DGO, GTO, HGO, MEX, ZAC	Jacoby (1891); FCB; USNM
Phyllotreta	*mexicana*	Jacoby	VER	Jacoby (1885)
Phyllotreta	*pusilla*	Horn	AGS, BC?, CHIH, DF, DGO, HGO, MOR, OAX, ZAC	Chittenden (1923); USNM, USNM-DGF
Phyllotreta	*subrugosa*	Jacoby	DF	Jacoby (1891)
Physimerus	*cordovensis*	(Jacoby)	VER	Jacoby (1886)
Physimerus	*femoralis*	(Jacoby)	VER	USNM
Physimerus	*scabrosus*	(Clark)	DGO, OAX, VER	Jacoby (1886); FCB
Platiprosopus	*pallens*	(Fabricius)	GRO, HGO, MOR, OAX, PUE, VER	Furth & Savini (1996); USNM
Plectrotetra	*clarki*	Baly	DF, DGO, HGO, MOR, OAX, PUE, SIN, SLP, TAMPS, VER	Jacoby (1884); FCB; USNM
Plectrotetra	*dohrni*	Jacoby	DF, DGO, HGO, PUE, VER, YUC	Jacoby (1884); FCB; USNM
Plectrotetra	*flohri*	Jacoby	MICH	Jacoby (1884)
Plectrotetra	*guatemalensis*	Jacoby	MOR	Jacoby (1891)
Plectrotetra	*inaequalis*	Jacoby	OAX, TAMPS, VER	Jacoby (1884); USNM
Plectrotetra	*multipunctata*	Jacoby	DGO?, MEX, MOR, OAX, VER	Jacoby (1891); FCB: USNM
Plectrotetra	*rugosa*	Jacoby	GTO	Jacoby (1884)
Plectrotetra	*sallei*	Jacoby	CHIS, TAB?	Jacoby (1884); FCB; USNM
Plectrotetra	*submetallica*	Jacoby	OAX, VER	Jacoby (1884)
Prasona	*viridis*	Baly	VER	Jacoby (1886)
Propiasus	*fulvus*	(Jacoby)	GRO	Jacoby (1892)
Pseudodibolia	*picea*	Jacoby	TAB	Jacoby (1891)
Pseudorthygia	n. sp.		CHIS	USNM-DGF
Pseudorthygia	*nigritarsis*	Jacoby	GRO, OAX, TAMPS	Jacoby (1891); USNM, USNM-DGF
Pseudorthygia	*unifasciata*	Jacoby	GRO	Jacoby (1891)
Psylliodes	*capitata*	Jacoby	GRO	Jacoby (1892)
Psylliodes	*convexior*	LeConte	BCS	Horn (1895); Furth & Savini (1998)
Psylliodes	*melanocephala*	Jacoby	DF	Jacoby (1891)
Psylliodes	*mexicana*	Jacoby	DF	Jacoby (1891)
Psylliodes	*sublaevis*	Horn	GRO	Jacoby (1891)
Resistenciana	*ornata*	(Jacoby)	PUE, VER	Jacoby (1884): FCB
Rhinotmetus	*depressus*	Clark	Mexico ?	Jacoby (1886)
Rhinotmetus	*flavovittatus ?*	Jacoby	Mexico ?	FCB
Rhinotmetus	*minutus*	Jacoby	VER	Jacoby (1892)
Rhinotmetus	*modestus*	Jacoby	GRO, MOR	Jacoby (1892); FCB

Genus	**Species**	**Author**	**Distribution**	**Source**
Scelidopsis	*rufofemorata*	Jacoby	TAMPS, VER	JACOBY (1888); USNM
Scelidopsis	*violacea ?*	Jacoby	GRO	JACOBY (1892)
Sphaeronychus	*fulvus*	(Baly)	DGO, TAMPS	JACOBY (1886); USNM
Sphaeronychus	*puncticollis*	(Jacoby)	GRO	JACOBY (1892)
Stegnea	*amplicollis*	(Jacoby)	GRO	JACOBY (1891)
Stegnea	*atra*	(Jacoby)	GRO	JACOBY (1891)
Stegnea	*guatemalensis*	(Jacoby)	GTO	FCB
Stegnea	*obliterata*	(Jacoby)	TAB	JACOBY (1891)
Strabala	*acuminata teapensis*	Blake	CHIS, TAB	BLAKE (1953); USNM
Strabala	*durangoensis*	Bechyné	DGO	BECHYNE (1955)
Strabala	*rotunda*	Blake	CHIS, COL, DF, GRO, JAL, NAY, NL, SLP, TAMPS, VER, YUC	BLAKE (1953); USNM; NHMB, ZSMC
Strabala	*rufa*	Illiger	CHIS, COL, DGO, GRO, OAX, PUE, TAB, VER	JACOBY (1884, 1891)
Strabala	*subcostata*	(Jacoby)	VER	JACOBY (1884)
Suetes	*niger*	Jacoby	GRO, MICH	JACOBY (1891); USNM
Syphrea	*abdominalis*	(Jacoby)	TAB, VER	JACOBY (1891)
Syphrea	*aeneipennis*	(Jacoby)	CHIS?, VER	USNM-DGF
Syphrea	*angustata*	Jacoby	COAH, GRO, PUE, VER	JACOBY (1891)
Syphrea	*balnearia*	Bechyné & Bechyné	GRO, MEX	USNM-DGF
Syphrea	*burgessi*	(Crotch)	MOR, OAX, TAMPS	USNM
Syphrea	*cyaneipennis*	(Jacoby)	GRO, HGO, JAL, SLP, TAB, TAMPS	JACOBY (1891); USNM
Syphrea	*flavicollis*	(Jacoby)	BCS, GRO, GTO, JAL, MOR, OAX, PUE	FCB; JACOBY (1884); RILEY, CLARK & GILBERT (2001); USNM
Syphrea	*frigida*	Bechyné & Bechyné	GRO, MEX	USNM-DGF
Syphrea	*minuta*	(Jacoby)	TAB, VER	JACOBY (1884); FCB
Syphrea	*parvula*	(Jacoby)	JAL, TAB, VER, YUC	JACOBY (1891); USNM
Syphrea	*pretiosa*	Baly	DGO, GRO, TAMPS	JACOBY (1891); USNM
Syphrea	*smithi*	(Jacoby)	OAX, TAB, TAMPS	JACOBY (1891); USNM
Syphrea	*sublaevipennis*	(Jacoby)	OAX, VER	FCB; JACOBY (1891)
Syphrea	*teapensis*	(Jacoby)	OAX, SLP, TAB, VER	JACOBY (1891); USNM-DGF; USNM
Systena	*abbreviata*	Jacoby	PUE	JACOBY (1902)

Genus	Species	Author	Distribution	Source
Systena	*basalis*	J. DuVal	VER	Furth & Savini (1998)
Systena	*bitaeniata*	LeConte	CHIH	USNM-DGF
Systena	*blanda*	Melsheimer	BC?, CHIH, JAL, MICH, NL, SIN, SLP?, SON, TAB, VER	Pallister (1953); USNM
Systena	*capitata*	Jacoby	DF, GTO,GRO, HGO?, MOR?, SLP?, VER?, ZAC?	Jacoby (1884); FCB; USNM
Systena	*championi*	Jacoby	GRO, MOR, OAX, VER	USNM
Systena	*contigua*	Jacoby	CHIS, GRO, GTO, HGO, OAX, SON?, TAMPS, VER?, ZAC	Jacoby (1884); USNM
Systena	*discicollis*	Clark	CAMP, CHIH, DF, DGO, GTO, JAL, MEX, MICH, TAB, TAMPS, VER?, ZAC	FCB; Jacoby (1884); USNM
Systena	*gracilenta*	Blake	NL	Blake (1933a); Furth & Savini (1998)
Systena	*laticollis*	Jacoby	GTO?	FCB?
Systena	*marginata*	Jacoby	PUE, VER	Jacoby (1884); USNM
Systena	*mexicana*	Jacoby	VER	Jacoby (1884)
Systena	*nigroplagiata*	Jacoby	AGS, CHIH, DF, DGO, GTO, GRO, JAL, MICH, MOR, OAX, PUE, VER	FCB; Jacoby (1884); Pallister (1953); USNM; USNM-DGF
Systena	*obliterata*	Pallister	CHIH	Pallister (1953)
Systena	*palmeri*	Jacoby	CHIS, COAH, DGO, GRO, SIN, SON, ZAC	Jacoby (1884); FCB; USNM
Systena	*pectoralis*	Clark	CHIS, GTO, OAX, VER	Jacoby (1884); FCB
Systena	*posticata*	Jacoby	VER	Jacoby (1884)
Systena	*puncticollis*	Jacoby	OAX	Jacoby (1884)
Systena	*s-littera*	(Linnaeus)	CHIS, GTO, TAB, VER	FCB; Jacoby (1884); USNM-DGF
Systena	*salvini*	Jacoby	CHIS	USNM
Systena	*scutellaris*	Jacoby	VER	Jacoby (1884)
Systena	*semivittata*	Jacoby	BCS, GRO, GTO, HGO, MEX, MOR, NL, OAX, SIN	Jacoby (1884); FCB; USNM; NHMB
Systena	*subcostata*	Jacoby	MICH, MOR, VER	Jacoby (1884); USNM
Systena	*subrugosa*	Jacoby	GTO, MICH, MOR	Jacoby (1884); USNM

Genus	Species	Author	Distribution	Source
Systena	*sulphurea*	Jacoby	CHIH, DGO, GRO, MOR, OAX	Jacoby (1891); FCB; USNM
Systena	*thoracica*	Jacoby	CAMP, HGO, PUE, QROO, TAB, VER	Jacoby (1884); FCB; USNM
Systena	*undulata*	Jacoby	AGS?, CAMP?, GRO?, GTO, MOR?, VER	Jacoby (1884); USNM
Systena	*variabilis*	Jacoby	CHIH, CHIS, COL, DGO, GRO, GTO, MICH, MOR, NAY, OAX, VER	FCB; Jacoby (1884); Pallister (1953); USNM; ZSMC
Systena	*viridilimbata*	Jacoby	GRO	Jacoby (1891)
Terpnochlorus	*americanus*	Bechyné & Bechyné	TAMPS	USNM
Tetragonotes	*vittatus*	(Clark)	VER	USNM
Trichaltica	*semihirsuta*	(Jacoby)	GRO, TAB, VER	Scherer (1960); FCB; USNM-DGF
Trichaltica	*tibialis*	(Jacoby)	Mexico	Wilcox (1975)
Walterianella	*biarcuata*	(Chevrolat)	CHIS, VER	Jacoby (1886); FCB
Walterianella	*durangoënsis*	(Jacoby)	CHIH, DGO	Jacoby (1892); FCB; Pallister (1953)
Walterianella	*gouini*	Bechyné	Mexico	Bechyne (1958b)
Walterianella	*humeralis ?*	(Fabricius)	Mexico?	FCB
Walterianella	*inscripta*	(Jacoby)	OAX, SLP, VER	Jacoby (1886); FCB; USNM
Walterianella	*oculata ?*	(Fabricius)	VER	FCB
Walterianella	*signata*	(Jacoby)	CHIS, JAL, TAB, TAMPS, VER, YUC	Jacoby (1886); FCB; USNM; USNM-DGF
Walterianella	*sublineata*	(Jacoby)	OAX, TAB, VER, YUC	Jacoby (1886); FCB; USNM
Walterianella	*tenuicincta*	(Jacoby)	SLP, TAB, VER	Jacoby (1886); FCB; USNM
Walterianella	*venustula*	(Schaufuss)	CHIS, COL?, GRO, JAL, MICH, MOR, NAY?, QROO, TAMPS?, VER, YUC	USNM

Bonner zoologische Beiträge	Band 54 (2005)	Heft 4	Seiten 239–245	Bonn, Oktober 2006

Frozen Chrysomelids from Alpine Glaciers – Witnesses of the Postglacial Resettlement[1]

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Abstract. In the last decades a significant retreat of alpine glaciers occurred. During these processes, some pieces of peat bogs melted out from below the glaciers. In this article, conclusions are discussed, which can be inferred from the Chrysomelidae fragments found in these pieces.

The first site is situated at Unteraar glacier in the Central Alps of Switzerland. The pieces of peat bogs are 3600 to 3800 years old and contained more than 5000 insect fragments. The Donaciinae remains showed a typical assemblage of a Cyperaceae fen peat. They contributed to a detailed assessment of the ecological conditions at this site 3600 years ago.

From below the Pasterze glacier, northeast of Grossglockner in Hohe Tauern, Austria, also pieces of peat bogs melted out. In the 8100 years old pieces, fragments of Chrysomelidae were found, which could be identified as *Oreina cacaliae* (Chrysomelinae). In the same pieces of peat bogs pollen of *Senecio* was found, too. With the *Oreina* fragments it was possible to narrow down the assignment to *Senecio fuchsii*, because *Oreina cacaliae* feeds only on this species of *Senecio*. But also interesting conclusions can be inferred concerning the postglacial resettlement. *Oreina cacaliae* has low dispersal ability. It persisted during maximum glacial extension in refugia far from its actual habitats, but managed to reach such a far site as the Pasterze 8100 years ago. This observation is contradictive to the theory of the "unfinished postglacial resettlement" due to lack of time. Other reasons for the restriction of the range of some species, which did not resettle obviously adequate habitats in the postglacial period, have to be discussed.

Key words. Holocene, beetle fragments, *Donacia, Oreina*, paleoecology, speed of dispersal, Pasterze, Unteraar glacier

1. INTRODUCTION

1.1. Retreat of glaciers and insect fragment analysis

In the last two decades a significant retreat of alpine glaciers could be observed. This retreat is not a new and singular event, it happened several times in the postglacial period (HORMES et al. 2001). There were several intervals, lasting several hundred years each, with warmer climate compared to the average temperature of the 20th century (Fig. 1). During those intervals peat bogs established in the wetlands after the retreat of the glaciers. During the next period of lower temperature, these peat bogs were covered by the growing glaciers. Nowadays, in the relatively warm climatic period, pieces of peat bogs are melting out from below the glaciers.

In peat bogs insect fragments can be found, which are preserved for several thousand to more than hundred thousand years. The most abundant sclerites are remains of beetles. In the last 30 years, the method of insect fragment analysis was established, mainly by G. R. Coope and his team, who published a lot of very interesting results from sites in southern Great Britain, Scandinavia and Northern America (COOPE 1986). Almost all of these investigations were made from areas around the southern fringe of the northern ice shield. In Central Europe there was also a large ice shield during glaciation, which covered large parts of the alps and partly the areas of the surrounding lowlands (Fig. 2). After the retreat of the glaciers many lakes and peat bogs emerged. In some of these places insect fragments were found and investigated, but only selectively and not systematically.

There are two main causes for this situation: Firstly, the insect fragment analysis is more difficult here, because in Central Europe the number of beetle species is three times the number of species in Great Britain or in the Scandinavian sites. Secondly, in Central Europe we had not such an outstanding person like G. R. Coope, who performed these investigations systematically and continually for more than three decades, with a lot of experience and many co-workers. Therefore, in most cases, insect fragments were found only occasionally by macrophytic remains screening and identified only occasionally.

This article shows the results of two interesting sites in Central Europe, where Chrysomelid fragments were preserved in peat bogs and melted out from alpine glaciers. The first site is situated in the Central Alps of Switzerland and was studied by an interdisciplinary project at the Institute of Geology at the University of Bern. The other sample derived from the Pasterze glacier near Grossglockner, located in Hohe Tauern, Austria. From

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[1] Paper presented to the 6th International Symposium on the Chrysomelidae, Bonn, Germany, May 7, 2004.

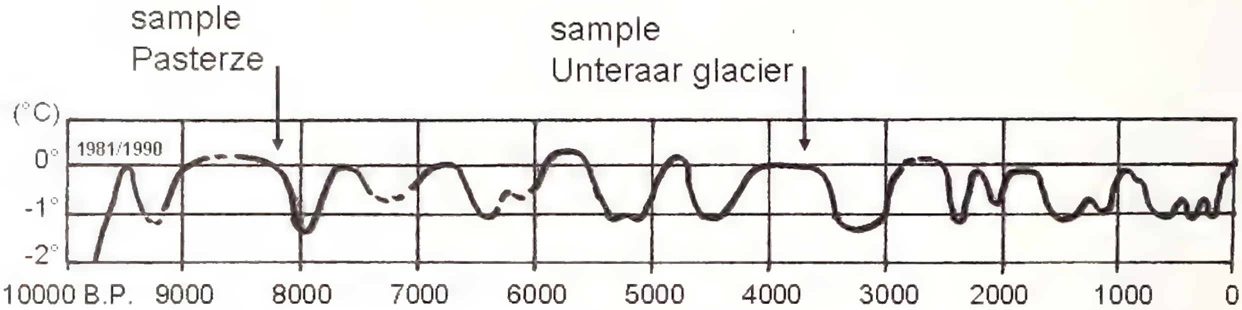

Fig. 1. Amplitude of the average summer temperature (May to September) in the Eastern Alps during the Holocene (graphics after SLUPETZKY et al. 1998).

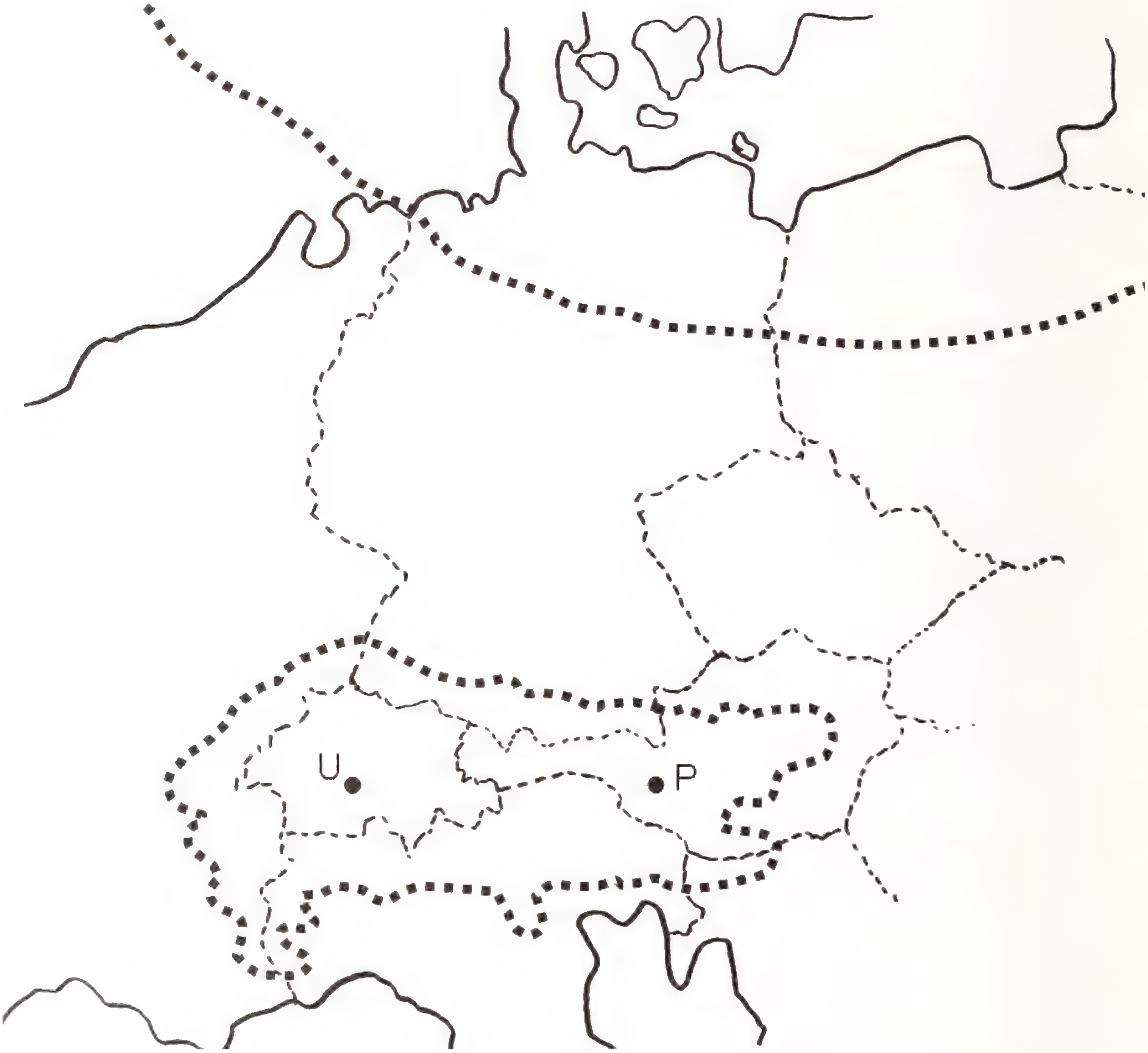

Fig. 2. Maximum extension of the Würm glaciers in Central Europe, 22000 B.P. U: Unteraar glacier, P: Pasterze glacier.

both sites interesting conclusions can be inferred from the Chrysomelidae fragments.

1.2. Coleoptera fragment analysis provides additional results to the method of pollen analysis

The method of pollen analysis, palynology, is well established for more than 80 years und revealed many interesting results, especially on glacial, interglacial and postglacial ecology. Also almost all sediments with Coleoptera remains contain a variety of pollen. There are two aspects to why Coleoptera fragments provide additional knowledge.

Firstly, with Coleoptera fragments it is possible to narrow down the climatic conditions at a special site better than by palynology. The MCR (Mutual Climatic Range) method, developed by ATKINSON et al. (1986), demonstrated its usefulness in many cases. It was used also in the study of the fragments from Unteraar glacier (JOST-STAUFFER 2000). Secondly, Coleoptera fragments can provide also more precise information about the vegetation, in addition to the results of palynology. Whereas the tree pollen looks very characteristic and can be assigned to the tree species in most cases, the pollen of many herbs can be assigned only to genus level or even to genus group. Therefore, fragments of monophagous or oligophagous beetles, like Chrysomelids, support useful additional information and can narrow down the results of pollen analysis to species level.

2. DONACIINAE FROM THE WESTERN ALPS

2.1. Site, materials and methods

From the Vorfeld of the Unteraar glacier, at 1920 m a.s.l., located in the Central Alps of Switzerland (Fig. 2), 3600 to 3800 years old pieces of peat bogs melted out. They contained about 5000 insect remains; most of them were beetle fragments. The items were assigned to the beetle families by the co-workers of a research project from the Institute of Geology at the University of Bern and identified as exact as possible. Then specialists of the identified Coleoptera families were contacted and asked, to check the identification and to do it more precisely, if possible. I was asked to check the Chrysomelidae fragments, except the Alticinae (which were checked by Manfred Döberl, Abensberg, Germany), and then 150 well prepared items were sent to me.

2.2. Results and discussion

The Chrysomelidae (except Alticinae) species found at that site belonged to the subfamily Donaciinae. The following species were determined (Table 1).

Table 1. Donaciinae identified from the Vorfeld of the Unteraar glacier, Switzerland. Nomenclature according to KIPPENBERG (1994).

Donacia clavipes Fabricius, 1792
Donacia semicuprea Panzer, 1796
Donacia aquatica (Linnaeus, 1758)
Donacia impressa Paykull, 1790
Donacia brevitarsis Thomson, 1884
Donacia brevicornis Ahrens, 1810
Donacia marginata Hoppe, 1795
Donacia obscura Gyllenhal, 1813
Donacia thalassina Germar, 1811
Donacia vulgaris Zschach, 1788
Donacia simplex Fabricius, 1775
Plateumaris sericea (Linnaeus, 1758)

Only a few fragments (most of them are elytra or the distal fragment of one elytron) could be assigned exactly to one species, but often it was possible to narrow down the identification to two or three species. Sometimes it was possible to identify the genus only. Other fragments could be clearly assigned to the subfamily Donaciinae, but could not be identified more precisely.

The species mentioned in Table 1 are distributed in the whole of Europe, or, at least, in large areas of Europe. Their habitats are in such a wide temperature range that these Donaciinae were not used for the MCR, like some other Coleoptera species found at the Unteraar glacier. But these Donaciinae fragments contributed to more precise information about that habitat at this site 3800 years ago. In combination with the other identified beetle species it can be inferred that that habitat contained a marshy wetland with different sedges and reeds with *Phragmites communis, Glyceria maxima, Sparganium simplex, Sparganium ramosum, Scirpus lacustris, Scirpus palustris, Carex rostrata* and other *Carex* sp. (Botanical nomenclature according to FISCHER et al. (2005)).

3. *OREINA* FROM THE EASTERN ALPS

3.1. Site, materials and methods

The Pasterze glacier is the largest glacier in the Eastern Alps. It is situated northeast of Grossglockner in Carinthia, Austria (Fig. 2). In 1990 to 1996 pieces of peat bogs and stems of coniferous trees (*Pinus cembra*) melted out. They were collected by G. Lieb and H. Slupetzky during routine measurements of the glacier and then investigated thoroughly (SLUPETZKY et al. 1998; GEISER 1998).

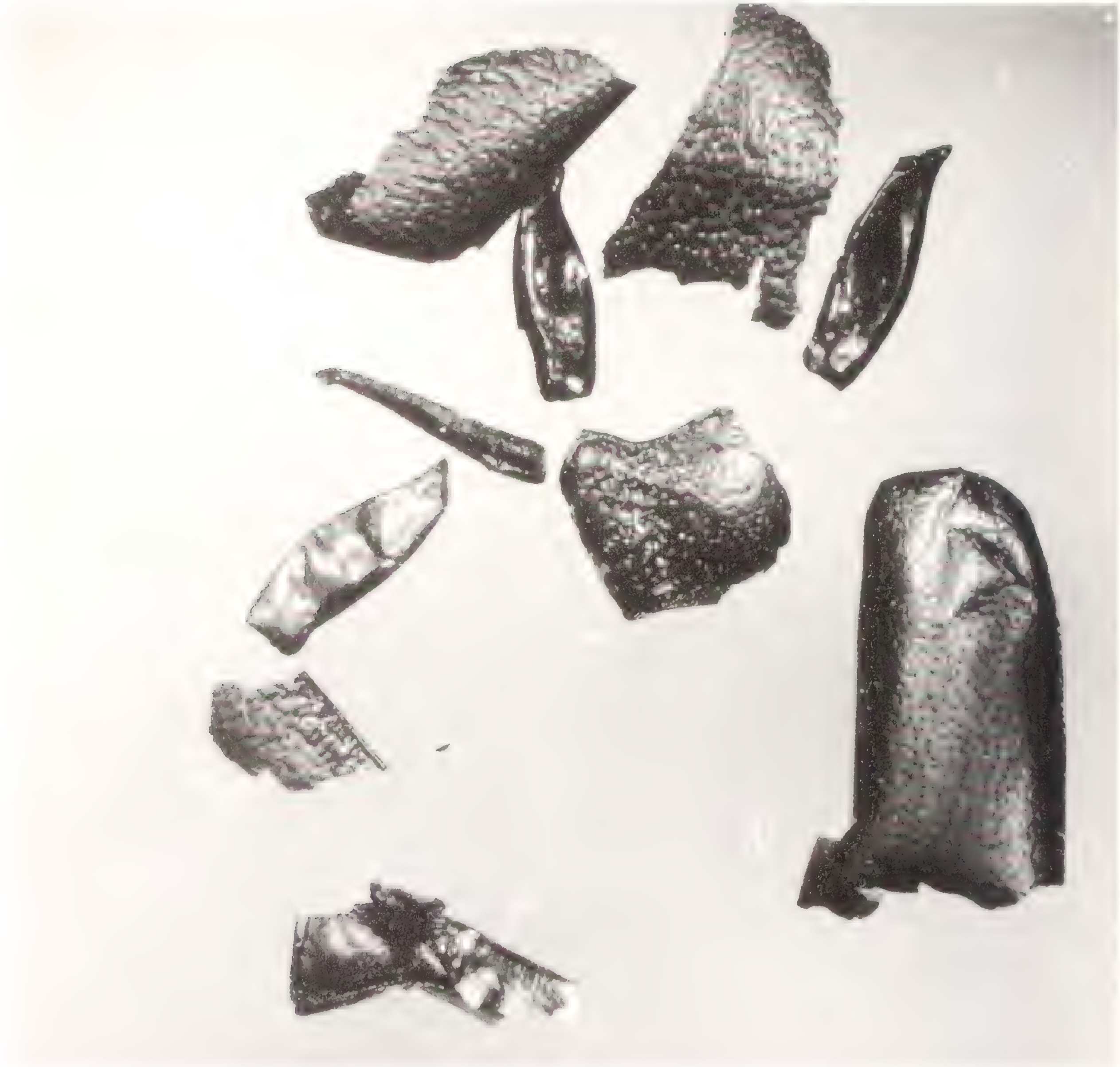

Fig. 3. Sample of 8100 years old *Oreina cacaliae* fragments, found near Pasterze glacier (Photo: J. Burgstaller).

By the screening for macrophytic remains some beetle fragments were found (Fig. 3). These pieces of peat bog also yielded a rich pollen assemblage. It was 8180 ± 70 years old. The original site of the peat is still covered by the Pasterze glacier, about 0.5 to 4 km upwards of the actual glacier terminus at approximately 2100 to 2300 m a.s.l.

The pollen analysis and the macrophytic remains analysis revealed that during a period from 9000 to 8100 years B.P. a mountain forest was established at that site. The main tree species was *Pinus cembra*, and the typical assemblage of vascular plants was found there, especially the tall herbaceous vegetation with *Senecio* species. The forest also contained several peat bogs. This ecosystem is typical for the Hohe Tauern, but nowadays situated several hundred meters lower. This time period was the largest interval of relatively warm climate in postglacial times (Fig. 1).

The beetle fragments are stored in the collection of the author, which is designated to the Biologiezentrum in Linz, Austria.

3.2. Results and Discussion

3.2.1. Result of the identification of these beetle fragments: *Oreina cacaliae.* The fragments found at that site could be identified as *Oreina cacaliae* (Schrank, 1785). They belong to a minimum of three individuals.

Subfossil fragments of that genus are very rare. The evidence that this species was established at this site 8100 years ago is a very interesting fact.

3.2.2. Biology and actual distribution area of *Oreina cacaliae.* The habitat of the leaf beetle *O. cacaliae* is constituted by tall herbaceous vegetation in mountainous areas in Europe at 800 to 2500 m altitude. On some sites with adequate microclimatic conditions it can also be found down to 600 m a.s.l. This species is ovovivipar, like other Chrysomelids at the same altitude. For pupal development and hibernation *O. cacaliae* stays in the soil. Imagines up to three years old are known (ROWELL-RAHIER 1992).

Oreina cacaliae is oligophagous on Asteraceae, it feeds only on *Senecio ovatus* (syn. *Senecio fuchsii*) and *Adenostyles alliariae* (HÄGELE et al. 1996; there exists a remarkable variation in the nomenclature of that species, which was called *Senecio fuchsii* for decades. Mostly it is named now *Senecio nemorensis* or *Senecio ovatus* or *Senecio nemorensis* ssp. *fuchsii.* There exist further names and combinations of names. But the plant species is always the same.). The preference of the altitudes mentioned above, and the restriction to these two host plants are the reason for the fragmentation of their distribution area.

Oreina cacaliae shows an aposematic colour with high variation. They synthesise chemical defence secretions out of secondary plant compounds from their host plants (PASTEELS et al. 1994). Therefore, their restriction to their host plant species has evolved long ago. There is no indication to a host plant change in the last 10 000 years.

3.2.3. Supplementation of the pollen analysis. In the pieces of peat bogs, which contained the *O. cacaliae* fragments, pollen of *Senecio* could also be identified. No *Adenostyles* pollen was found. Therefore it can be inferred that the *Senecio* pollen identified at the Pasterze belong to *Senecio fuchsii.*

3.2.4. Glacial refugia of *Oreina.* The majority of today's distribution area of *O. cacaliae*, especially in the Alps, was covered with glaciers until 13 000 years ago. In many other locations of the actual range it was also impossible for the host plants to settle there, due to climatic reasons. Therefore, during the periods of large glacier extension, the majority of the populations of *O. cacaliae* had to persist in refugia far from their actual habitats. Figure 2 shows the maximum of the glacier extension in Central Europe at the period of Würm, 22 000 years ago.

3.2.5. Dispersal ability of *Oreina cacaliae* and its host plants. The host plants have very high dispersal ability, as usual in Asteraceae, which disperse easily with their pappi. Therefore they reached adequate habitats quickly during the periods of retreating glaciers and during their growing periods, also. On the other hand, *O. cacaliae* has relatively low dispersal ability. This is very difficult to observe directly, but there are some facts that support this assumption:

Field studies in the Swiss Alps showed that the adults moved only a few meters during summer, and a high percentage of individuals were recaptured in the next year, less than 5 m from the places where they were marked (ROWELL-RAHIER 1992).

Coloration of *O. cacaliae* is highly variable, even within one population. But the set of colour variations is very typical for different regions within the whole area of distribution. This indicates that the populations are isolated for a long time.

3.2.6. Dynamics of the postglacial resettlement. The majority of the animal and plant species of Central Europe have high dispersal ability. This is due to more than 50 periods of growing and retreating glaciers. The habitats shifted to the south and then to the north within a few thousand years. Therefore species with high dispersal ability had more chance to survive the Quaternary Ice Age. Species with high dispersal ability will spread to their habitats in Europe within a few 100 years (GEISER 1997). But also some species with relatively low dispersal ability managed to survive the climatic and therefore the habitat fluctuations. The species that didn't manage this became extinct in Central Europe.

The retreat of the glaciers after their maximum extension started about 20 000 B.P. This retreat was interrupted by some colder climate intervals. At 10 300 B.P. the glacier dimensions were similar to the dimensions in the 20th century. There were some small fluctuations in the Holocene (Fig. 1). The most recent retreat of the glaciers started in 1860, interrupted by a short growing period at 1920. Nowadays, a significant retreat can be observed since 1982.

The longest warm period lasted from 9000 to 8000 B.P. At a site that is still covered by the Pasterze glacier, a mountain forest with *Pinus cembra* could establish. The fragments of *Oreina cacaliae* show that even a species with such low dispersal ability could reach this remote site within a few thousand years.

3.2.7. Is "not yet finished postglacial resettlement" a relevant explanation for restricted distribution areas? There are several species known with a very patchy distribution area and adequate habitats in between. Some of these gaps in distribution are explained by "not yet finished resettlement" (since HOLDHAUS 1954) that implies that this is due to the lack of time in the postglacial period to reach that habitats. On the contrary, the example of *Oreina cacaliae* shows that a species with low dispersal ability could reach remote habitats within a few thousand years.

The extension of a definite distribution area of a definite species always changes dynamically, with lower or higher amplitude. Therefore, resettlement is never "finished". The restriction of distribution areas can be explained more probably as a result of the interaction of the following reasons:

- low dispersal ability
- low competitive ability
- highly specialised ecological demands
- geographical barriers (from the point of view of the species)
- and last, but not least, our lack of knowledge about the detailed biology and ecological demands of the definite species.

The dynamics of dispersal and the real process of the postglacial resettlement is inferred indirectly only, in most cases. Modern molecular methods, such as isoenzyme electrophorese (SCHMITT 2000) or DNA analysis, are very useful, but indirect, too. Real items on a real site with a definite age have to match the theory, if not the theory has to be revised.

Our knowledge about the causes of distribution, about postglacial resettlement and changes of climatic and other ecological conditions during the Quaternary, depends on pieces of a dazzling, but highly interesting puzzle, which is composed of many items and methods. The more such items we find and examine with different methods we have, the clearer our idea of the postglacial ecology will be.

Acknowledgements. All these interesting results derived from Chrysomelidae fragments, which were sampled and extracted by other scientists: the Doncaciinae fragments I received from Dr. Monika Jost-Stauffer were in excellent preparation and packing (that cannot be taken for granted!). Also, the cooperation with her and the Institute of Geology of the University of Bern was excellent.

The pieces of peat bogs, which contained the *Oreina* fragments, were sampled by Univ. Prof. Dr. Gerhard Lieb (Institute of Geology, University of Graz). The fragments were detected by Univ. Prof. Dr. Robert Krisai (Institute for Botany, University of Salzburg). Univ. Prof. Dr. Heinz Slupetzky (Department of Glaciology at the Institute of Geography, University of Salzburg) coordinated these investigations at the Pasterze glacier and supported me with useful information. He also initialized the cooperation with Mag. Johann Burgstaller (Salzburg), an experienced photographer of crystals, who managed to photograph that shiny surface of the *Oreina*-fragments.

My husband was, as always, a meticulous proof-reader and made a lot of critical comments. It is an inestimable advantage to be criticised by a real friend and expert Coleopterologist.

Cordial thanks to all these colleagues.

ZUSAMMENFASSUNG

Die Klimaerwärmung der letzten beiden Jahrzehnte hat zu einem Rückzug der Alpengletscher geführt. Bei diesen Schmelzprozessen wurden an mehreren Stellen der Alpen unter den Gletschern gelegene Torfstücke herausgeschwemmt. Die vorliegende Arbeit berichtet über die Ergebnisse von zwei Fundstellen, an denen subfossile Chrysomelidenreste gefunden wurden.

Die erste Fundstelle befindet sich am Unteraargletscher in den Schweizer Zentralalpen. Die ausgeschwemmten Torfstücke waren 3600 bis 3800 Jahre alt und enthielten über 5000 Insektenreste, die im Rahmen eines Projektes des Geologischen Institutes der Universität Bern untersucht wurden. Die Autorin überprüfte und bestimmte die Reste der Unterfamilie Donaciinae. Die Artzusammensetzung entsprach der typischen Donacien-Fauna eines Cyperaceen – Flachmoores. Diese Befunde trugen zusammen mit den anderen Käferresten zu einer sehr genauen Einschätzung der ökologischen Verhältnisse an dieser Stelle der Alpen im genannten Zeitraum bei.

Die zweite Fundstelle befindet sich unter der Pasterze nordöstlich des Grossglockners (Hohe Tauern, Österreich). Die herausgeschwemmten Torfstücke enthielten Reste eines 8100 Jahre alten Bergblattkäfers: *Oreina cacaliae*. Dieser Fund einer oligophagen Chrysomelidenart trägt zu einer Präzisierung der botanischen Befunde durch Pollen- und Großrestanalyse bei. Dadurch ist die Aussage möglich, dass es sich bei den ebenfalls in dieser Probe nachgewiesenen *Senecio*-Pollen um die Art *Senecio fuchsii* handelt. Weiters liefert dieser Fund einer wenig ausbreitungsfreudigen Art an einer Stelle, die von den Glazialrefugien dieser Käferart weit entfernt ist, einen interessanten Hinweis über den Verlauf bzw. die Geschwindigkeit der postglazialen Wiederbesiedlung.

Die eingeschränkte Verbreitung mancher Arten, trotz Vorhandenseins zahlreicher (anscheinend!) geeigneter Habitate wird immer wieder mit einer „nicht abgeschlossenen nacheiszeitlichen Wiederbesieldung" erklärt, mit dem Argument, dass seit dem Ende der letzten maximalen Gletscherausdehnung im Hochwürm vor 20 000 Jahren die Zeit noch nicht ausreichte für die Arealausweitung auch von wenig ausbreitungsfreudigen Arten. Wenn aber Arten wie *Oreina cacaliae* bereits vor über 8000 Jahren die entlegensten Habitate in den Alpen besiedelt haben, dann erscheint diese Theorie wenig

stichhaltig und die Ursache der eingeschränkten Verbreitungsgebiete muss neu diskutiert werden.

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Bonner zoologische Beiträge	Band 54 (2005)	Heft 4	Seiten 247–252	Bonn, Oktober 2006

Striking Differences in Behaviour and Ecology Between Populations of *Chrysomela lapponica*[1]

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Abstract. Willows and poplars have been suggested as ancestral host plants of *Chrysomela* species (Coleoptera, Chrysomelidae). In the leaf beetle species *C. lapponica*, some populations are specialized on willow species, but others on birch. In this paper, we review results from previous studies on ecological interactions between *C. lapponica* and its biotic and abiotic environment. We found striking differences between individuals of different populations in morphological traits, chemical composition and origin of larval glandular secretions, feeding habits, host preferences and feeding stimulants of larvae and adults. Furthermore, we discovered significant between-population differences in bottom-up, host plant depending performance parameters such as developmental time, body mass, and mortality as well as differences in top-down effects such as defensive secretions against predators, parasitoids and pathogens. We review results of hybridization experiments between different populations and then address the question whether the different host-specific populations of *C. lapponica* represent more than one species.

Key words. Speciation, post zygotic isolation, host shift, larval defence, top-down effect, bottom-up effect, willow, birch, *Chrysomela lapponica*

1. INTRODUCTION

Leaf beetle species belonging to the *Chrysomela interrupta*-group, a subtaxon of the Chrysomelina, show variation in host plant specialization. Some species are specialized to feed and oviposit on willows (Salicaceae), while others live only on birch or alder (Betulaceae) (BROWN 1956; GROSS 1997; GROSS et al. 2004b; GROSS & HILKER 1995; TERMONIA et al. 2001; TERMONIA & PASTEELS 1999). Among the *C. interrupta*-group, populations of *C. lapponica* are known to be exclusively specialized on either birch or on willow. *Chrysomela lapponica* is distributed almost continuously in Northern Europe (e.g., Finland, Sweden, Norway, Russia, Baltic States) (GROSS 2001; GROSS et al. 2004b; HILKER & SCHULZ 1994; MACHKOUR M'RABET 1996; ZVEREVA et al. 1995) and is divided by the boreal coniferous forest belt from the populations in Central Europe, which are distributed patchily in mostly higher or colder regions such as Germany, Czech Republic, Poland, Northern Italy and France (GROSS 1997; GROSS et al. 2004c; HILKER & SCHULZ 1994). The larvae and adults from Northern Europe feed and oviposit only on some willow species, while most of the Central European populations are monophagous on birch (GROSS 1997; GROSS & HILKER 1995). The aim of this review is to summarize information about the ecological factors, which may have driven the divergent evolution of host plant specialization in the Northern and Central European populations of *C. lapponica*. To elucidate this matter, we compared two populations of *C. lapponica*, which are specialized on different host plants. One of the populations occurs in Finnish Lapland and feeds mainly on the willow *Salix borealis*. The other population, feeding exclusively upon the birch *Betula pubescens*, was observed in the Czech Republic, close to the city of Marianske Lazne. Both, birch and willow hosts occur sympatrically in the habitats of the Finnish and Czech beetles. We conducted field and laboratory investigations over nine years, using morphological, chemical, physiological and microbiological analyses to determine whether or not these host specialized populations were one and the same species.

2. OVERVIEW OF PRESENT RESULTS

2.1. Morphological differences

The adults of birch-feeding populations of *C. lapponica* differ in the colour patterns of their red and black elytra compared with their willow-feeding counterparts from Northern Europe and Central Europe. While the ratio of black and red colour is about fifty-fifty in the Czech population, the relative size of the black marks of the Finnish beetles' elytra is significantly higher (GROSS et al. 2004c). The tibiae of the adults' first leg pair of the Czech population are predominantly black coloured, whereas the tibiae of the Finnish beetles are mainly red. Sometimes complete blue morphs occur spontaneously within the populations of Central Europe, but never in the populations from Northern Europe.

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[1] Paper presented to the 6th International Symposium on the Chrysomelidae, Bonn, Germany, May 7, 2004.

The larvae of the Chrysomelina and Phyllodectina possess nine pairs of dorsolateral defensive glands located on thorax and abdomen. When disturbed, the glandular reservoirs can be everted, and subsequently be inverted with the help of specialized retractor muscles. The reservoirs are filled with volatile compounds (GARB 1915; HINTON 1951). However, there are striking chemical differences between the Czech (birch-feeding) and Finnish (willow-feeding) populations of *C. lapponica* in the chemical composition of these larval secretions. Gas chromatography coupled with mass spectrometry (GC-MS) was used to identify the composition of the larval secretions and to quantify their amounts. The secretion of the birch-feeding larvae from the Czech population contained carboxylic acids and carbonic acid esters (Fig. 1A) which were synthesized *de novo* and esterified with alcohols taken from the plant (SCHULZ et al. 1997). However, like in all other willow-feeding *Chrysomela*-species, the secretion of the willow-feeding larvae from Finland contained salicylaldehyde as the major component (Fig. 1B). In all systems studied to date, salicylaldehyde is derived from salicin uptaken from willow leaves by the larvae (GROSS 1997; GROSS et al. 2002; GROSS & HILKER 1995; PASTEELS et al. 1988). Interestingly, the two *C. lapponica* secretion types can easily be distinguished in the field according to their different odours. The secretion of the willow-feeders smells like fruit salad, while the birch-feeder's secretion smells like almond liqueur.

2.2. Ecological interactions

First, we investigated the bottom-up effects, which are influenced by the first trophic level, the host plants. To assess these effects, we used different parameters for measuring the performance of the beetles on different plants. These were mortality, developmental time, volume of the larval secretion, fecundity and body weight of the neonate larvae and adults. Secondly, we investigated the top-down effects, that is, those influenced by the third trophic level, like predators, parasitoids and pathogens. An interspecific competition (within the 2nd trophic level) could not be detected (GROSS 2001).

Bottom-up effects. The adults of both Finnish and Czech populations prefer their natural host plant for feeding and oviposition over that of the host plant of the other population (GROSS & HILKER 1995). While there was neither a difference in fecundity nor in body weight of neonate larvae, we observed significant differences in mortality when the beetles were reared on their natural host plant versus the host plant of the other population without enemies in the laboratory (GROSS et al. 2004a). While a few individuals of the birch-specialized population could be reared on willow, all neonate larvae of the willow-specialized population died after having been transferred to birch (GROSS et al. 2004a). When individuals of the two *C. lapponica* populations were reared on their natural host plants, the birch specialists suffered higher mortality than the willow specialists (GROSS et al. 2004a). Probably as a consequence of host plant specialization in *C. lapponica*, there was a significantly shorter developmental period for the Finnish beetles on willow compared to that of the Czech beetles feeding upon birch (GROSS et al. 2004a). If the "slow-growth, high-mortality" hypothesis (WILLIAMS 1999; DENNO et al. 1990) applies to *C. lapponica*, the prolonged developmental time might be detrimental to the birch-feeding larvae, because they would remain in the more vulnerable larval stages for a longer time period. Higher mortality could result from higher predation, parasitism or higher microbial infection rates. Fecundity does not differ between individuals of both populations. However, a smaller volume of larval secretion is produced by the birch-feeding larvae (GROSS et al. 2004a).

Top-down effects. Laboratory experiments showed that both types of larval secretions (above-mentioned) of *C. lapponica* are highly effective against generalist predators with chewing-biting mouthparts like coccinellids, but ineffective against generalists with sucking-piercing mouthparts (GROSS 2001). However, significant differences exist between both secretion types in the effectiveness towards pathogens. The secretion of the willow-feeding larvae was highly effective against various microorganisms, especially against the entomopathogenous fungus *Metarhizium anisopliae*. When applied directly onto the blastospores, fungal germination and growth was greatly inhibited by the main component of the secretion, salicylaldehyde. Additionally, physiological quantities of volatile salicylaldehyde were shown to reduce germination and growth of *M. anisopliae* up to 45 mm around the application site (GROSS et al. 2002). In contrast, no antimicrobial activity was found in the larval secretion of the birch-feeding population. Laboratory results supported field observations because no infected ontogenetic stages of *C. lapponica* were found in Finland, while infected larvae and pupae were collected in the Czech Republic (GROSS 2001).

It was previously known that salicylaldehyde, the main component of the secretion of willow-feeding larvae, did not repel but instead attracted a specialized enemy, the predaceous hoverfly *Parasyrphus nigritarsis* (KÖPF et al. 1997). Therefore, laboratory studies were conducted to evaluate the response of *P. nigritarsis* larvae towards the salicylaldehyde-free secretion of the birch-feeding larvae. *Parasyrphus nigritarsis* hunted for larvae of both populations, but the secretion of the birch-feeding larvae was significantly less attractive than that of the willow-feeding larvae. Faeces of the willow-feeding larvae attracted this predator, as well. However, *P. nigritarsis* did not respond to faeces of larvae fed with birch leaves. In the field, *P. nigritarsis* is common in both habitats, but infested egg batches were found only on willows. The hover fly was never observed preying on individuals of the birch-feeding population (GROSS et al. 2004b).

In general, a higher percentage of the willow-specialized *C. lapponica* were found to be parasitized compared with the birch specialists. Both, in 1999 and in 2000, the percentage of parasitation by the phorid fly *Megaselia opacicornis* of the willow-specialized *C. lapponica* specimens was significantly higher than of the birch specialists. This parasitoid cannot be repelled by larval secretions. Parasitization by other species was low in each year both for birch and willow specialists (GROSS et al. 2004b). The parasitoids that were reared from parasitized *C. lapponica* larvae or pupae are all known to only develop in *Chrysomela* species (COX 1994; DISNEY et al. 2001; ZVEREVA & KOZLOV 2000). The influence of host plants or larval secretions on the host-finding behaviour of parasitoids was tested in field experiments in Finland. These experiments showed that parasitoids use both chemical signals of the willows (GROSS et al. 2004b) and volatile secretions of the willow-feeding larvae as kairomones for host localization (ZVEREVA & RANK 2004).

Abiotic factors (e.g., temperature, radiation). The adaptive value of the elytral colouring, one of the most conspicuous differences between the adults of both populations of *C. lapponica*, was examined. Adults of the Finnish and other populations from Northern Europe were found to be significantly darker in colour than their Czech counterparts (GROSS 1997; GROSS et al. 2004c; ZVEREVA et al. 2003). As a result, Finnish beetles heated up more quickly when exposed to insolation. The dark colouring of the Finnish beetles may therefore be an adaptation to their colder environment with shorter seasonal vegetation periods (GROSS et al. 2004c). Also, some endogenous factors were found to differ between the populations. Batch calorimetry experiments gave evidence that the specific metabolic rate during hibernation at low temperatures was lower in the Czech beetles. Individuals of the Czech population may have to cope with higher and fluctuating winter temperatures. Additionally, the walking speed and the feeding activities of the Finnish beetles were higher at low temperatures when compared to the Czech beetles (GROSS et al. 2004c).

Crossing experiments. Very few examples of host race formations are known in chrysomelids. Among them are the *Gallerucella nymphaeae* species complex (HIPPA & KOPONEN 1986; NOKKALA & NOKKALA 1994; NOKKALA & NOKKALA 1998; PAPPERS et al. 2002b; PAPPERS et al. 2002a) and the *Lochmaea caprea* (Kreslavskiy & Mikheyev 1994). However, unconfined hybrid formation was possible between the host races in these examples. Fatouros *et al.* (unpublished results) tried to interbreed individuals of *C. lapponica* from Finland (willow-feeders) and the Czech Republic (birch-feeders) in the laboratory. Only a unidirectional hybrid formation between females from the Czech Republic and males from Finland succeeded, whereas the reciprocal pairings produced no offspring. But the resulting hybrid larvae could not survive. By keeping the ability to feed on only willow, they were doomed to death on birch, as their birch-feeding mothers laid the eggs exclusively on birch leaves. This represents possibly a new postzygotic isolation mechanism (Fatouros et al. in press).

3. DISCUSSION

This review focuses on the ecological factors which selectively influence phenotypically different individuals of *C. lapponica*. But natural selection is only one of several factors driving the evolution of organisms (MAYR 1997). Other random evolutionary factors like genetic drift and mutation were not investigated.

Influence of biotic selection factors. The influence of biotic selection factors on the two investigated populations of *C. lapponica* is summarized in Table 1. No competition between *C. lapponica* and other herbivores could be detected in both habitats and upon both host plants (GROSS 2001). The respective host plant species had an effect on the performance of the leaf beetle. Birch-feeding larvae feeding under standardized conditions on leaves of their natural host plant, *B. pubescens*, developed more slowly than willow-feeding larvae reared on leaves of their natural host plant, *S. borealis* (GROSS et al. 2004a). This laboratory result, however, may not be of ecological significance, because developmental time increases with higher temperatures (HONĚK & KOCOUREK 1988; HOWE 1967). Therefore the adverse effect of the birch on the beetles' developmental time could be compensated for, since the mean temperatures during the vegetation period in the Czech Republic were significantly higher than in Finland (GROSS et al. 2004c). If this is not the case, the prolonged developmental time might be detrimental to the birch-feeding larvae, because they remain in vulnerable immature stages for a longer period of time. Higher mortality could result from enhanced predation, parasitation or microbial infection (HÄGGSTRÖM & LARSSON 1995; WILLIAMS 1999).

Birch-feeding larvae were also found to have reduced volumes of secretions. This had obviously no effect on the larvae, because even little quantities of secretion were highly effective against ladybird beetles (GROSS et al. 2004a). Apart from directly affecting the beetles development and larval secretion quantity, the host plant may also have an indirect influence on top-down effects by determining the chemical composition of the larval defence secretions. A laboratory experiment showed that willow-feeding larvae were better defended against pathogens than birch-feeding larvae due to the salicylaldehyde in the secretion of the willow-feeding larvae (GROSS et al. 2002).

Although birch-feeding larvae seem to face a number of disadvantages as a result of feeding on an apparently suboptimal host, there is evidence for a trade-off: the secretion of birch feeding larvae was shown to be less attractive to the specialist predator, *P. nigritarsis,* than the salicylaldehyde-containing secretion of larvae of the willow feeding populations (GROSS et al. 2004b). Consequently, our data suggest that the secretion of the birch-feeding larvae provides a selective advantage, due to a decreased predation pressure by specialists on eggs and larvae.

Influence of abiotic selection factors. Individuals of *C. lapponica* in Finland and the Czech Republic live in environments, which differ in their temperature conditions and in the length of their vegetation period. Those adult beetles living in colder environments (Finland) benefit from their darker elytral colouring by heating up more rapidly. The higher body temperatures attained positively affect their walking and feeding behaviour (GROSS et al. 2004c). Additionally, their temperature range for feeding and walking activity is lower than in their counterparts living in warmer environments (Czech Republic). In contrast, the lower specific metabolic rates of the Czech beetles at low temperatures are favourable during hibernation, because their energy resources decrease more slowly than the energy resources of the Finnish beetles. The elytral colouring as well as internal physiological factors lead to an optimal adaptation to temperature conditions in the different habitats of *C. lapponica* in Central and Northern Europe (GROSS et al. 2004c).

Summarizing the effects of the three trophic levels on *C. lapponica*, plant (i.e., host plant species), herbivorous insect (i.e., competitors), and antagonists (i.e., predators, parasitoids, and pathogens), the following evolutionary scenario arises. Since larvae adapted to willow have a shorter developmental period if reared on willow than birch-feeders reared on birch, willow is obviously a better food plant than birch. Competition between *C. lapponica* and other herbivores could not be detected. Consequently food does not seem to be limiting. Feeding on willow benefits larvae due to the antimicrobial activity of their willow-derived salicylaldehyde-rich secretion. The secretion protects willow-feeding larvae against fungal infection. Birch-feeding larvae are more vulnerable to fungal infections since their secretion lacks significant antifungal activity. Nevertheless, feeding on birch has a major advantage as it allows those larvae to produce a secretion which is significantly less attractive to specialist predators like the hoverfly, *P. nigritarsis,* than the secretion of the willow-feeding larvae. The different elytral colouring and temperature optima traits of the imagoes from both populations appear to be highly adaptive to the extant environmental conditions in their current ranges.

Is the willow the ancestral host plant? The results reviewed here suggest that the ancestral host plant of *C. lapponica* belonged to the Salicaceae: While individuals of the birch-feeding population of *C. lapponica* can obviously cope with the secondary metabolites of the willow, as they are still able to develop from larvae to adults when fed with willow leaves, individuals of the willow-feeding population cannot survive when fed with birch leaves (GROSS et al. 2004a). When reared on *Salix fragilis* in the laboratory, birch-feeding larvae produce trace amounts of salicylaldehyde in their secretion (GROSS 1997; HILKER & SCHULZ 1994), suggesting that this ability could be a vestige of the ancestral pathway. These findings indicate that the birch-feeding population has adapted very well to its new host-plant in the interim, because its performance is negatively affected when reared on willows (GROSS et al. 2004a). Further studies of the natural enemies of the Nearctic species within the *C. interrupta*-group feeding upon alder have to be conducted in order to elucidate the convergent or reversal host shifts between Betulaceae and Salicaceae, as it was suggested by TERMONIA et al. (2001).

Do the birch feeding populations represent a host race or a new species? According to our findings obtained over the past nine years of field and laboratory experimentation, we conclude that the pronounced and consistent differences in morphology, ecology and ethology between most birch-feeding and willow-feeding populations of *C. lapponica*, the species *C. lapponica* should be divided in two distinct species. With regard to ecologically important traits like feeding specialization and oviposition behaviour, one may distinguish between a birch-feeding species, to which most of the investigated populations from Central Europe belong (Germany, Czech Republic, Poland and France (Massif Central)), and a willow-feeding species, which includes all populations from Northern Europe (Finland, Norway, Russia) and one population from France (Queyras).

Acknowledgements. The authors greatly appreciate Monika Hilker (Berlin), Horst Kippenberg (Herzogenaurach), Seppo Neuvonen (Kevo Subarctic Research Station, Finland), Jacques Pasteels (Belgium), Andreas Vilcinskas (Gießen), and Andrzej Warchalowski (Poland). We thank

Meike Brück (Walldorf) and two anonymous reviewers for important remarks and linguistic improvements.

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Bonner zoologische Beiträge	Band 54 (2005)	Heft 4	Seiten 253–259	Bonn, Oktober 2006

Parameres – Similarities and Differences in Chrysomelidae and Cerambycidae (Coleoptera)[1]

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Abstract. Parameres, or lateral lobes, of the male copulatory organ are present in many insect groups, while in others they are reduced or completely lacking. Nearly all long-horned beetles have parameres, while only the leaf beetle subtaxa Megalopodinae, Zeugophorinae, Orsodacninae, Bruchidae, Sagrinae, Donaciinae and the genus *Timarcha* possess them. In these taxa, parameres can consist of one or two lobes, can be very long or quite short, and the number and density of their setae can vary. Based on this wide morphological variability, we draw conclusions on the phylogeny of Chrysomeloidea and then formulate a hypothesis accounting for the probably diverse functions parameres might have in both the long-horns and in the leaf beetles. One recent discovery is the existence of minute openings in the surface of the parameres, which may indicate the presence of glands. These structures are illustrated and their possible functions discussed.

Key words. aedeagus, male genitalia, morphology, phylogenetics

1. INTRODUCTION

1.1. General

Surprisingly there are only few papers on parameres, or lateral lobes, of the male aedeagus found in many beetles. Although parameres are quite complex and species-specific, their functional role is largely unknown, even though these structures have at least one known function. Hubweber (unpubl. data) used genital characters, including those of the aedeagal parameres in an analysis of the phylogenetic relationships among the subfamilies of the Cerambycidae. Because some Chrysomelidae groups also possess parameres, we expanded this initial survey to include both the Cerambycidae and Chrysomelidae. We then compared character states of parameres between the two groups. In addition, we briefly examined the function of the parameres and then went on to discuss the discovery and possible significance of minute holes indicative of glandular openings on the surface of the parameres.

1.2. Terminology

Over the decades many genitalic structures in beetles have been described, mostly for taxonomic purposes. But not all entomologists have followed the same terms in the description of these different structures. The term "aedeagus" for example, is often used synonymically with "median lobe", but we use it to describe the median lobe and the tegmen together. In our opinion the latter structure, the tegmen, consists of the parameres (or lateral lobes) and the basal piece or tegminal struts, connected by the tegminal ring.

1.3. Literature Review

VERMA (1996) and CHEN (1985) illustrate the loss of the parameres within the Chrysomelidae. While Megalopodinae, Zeugophorinae, Orsodacninae, Bruchidae, Sagrinae, Donaciinae and *Timarcha* show a typical tegmen, the tegminal ring and therefore also the parameres, are reduced in all other subfamilies. *Stenhomalus* is the single cerambycid genus known lacking parameres (WU & JIANG 1993). Another question concerning the homology of genitalia in chrysomelids is the single genus within Chrysomelinae, *Timarcha*, showing a complete tegminal ring with parameres.

HARNISCH (1915) examined the male genital system of some chrysomelids including *Plateumaris sericea*. Harnisch observed that in this species the tegmen remains outside the female genitalia during copulation, acting as a grasping organ and lever. This case is quite similar to Bruchidae as DÜNGELHOEF & SCHMITT (2006) show, but they observed slight movements in *Acanthoscelides-obtectus*-parameres during copulation. Similar movements of the parameres have been observed in the carabid beetle *Pasimachus punctulatus* (ALEXANDER 1959) and in the coccinellid beetle *Cycloneda sanguinea* (EBERHARD 1985). These movements could serve as a kind of stimulation, supporting the "cryptic-female-choice"-hypothesis (EBERHARD 1985, 1996).

KINGSOLVER (1970) observed that in *Mimosestes sallaei* (Bruchidae) the parameres are known to enter the female vaginal tract during copulation. In all other bruchids investigated, the parameres obviously "serve as guides to position the median lobe opposite the vaginal opening."

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[1] Paper presented to the 6th International Symposium on the Chrysomelidae, Bonn, Germany, May 7, 2004

EBERHARD (1993) examined the functional role of parameres in the scarabaeid species, *Macrodactylus costulatus*. He described a "foot-in-door-sac" that is inflated right beneath the apex of the parameres and thus occupies the entrance to the female genitalia and can trigger the vulva to open.

2. MATERIALS AND METHODS

We examined dry museum specimens (from the ZFMK collection) and some field-collected fresh specimens. These latter specimens were collected mostly in summer 2002 near Dahlem and Blankenheim in the Eifel mountain region (about 70 km SW of Cologne).

The structures of the aedeagi of 1-5 specimens of the following species have been studied:

Cerambycidae

Cerambycinae: *Stenopterus rufus* (Linnaeus, 1767), *Obrium brunneum* (Fabricius, 1792), *Pyrrhidium sanguineum* (Linnaeus, 1758), *Plagionotus detritus* (Linnaeus, 1758)

Lamiinae: *Dorcadion pedestre* (Poda, 1761), *Acanthocinus aedilis* (Linnaeus, 1758), *Agapanthia villosoviridescens* (Degeer, 1775)

Lepturinae: *Dinoptera collaris* (Linnaeus, 1758), *Carilia virginea* (Linnaeus, 1758), *Grammoptera ruficornis* (Fabricius, 1781), *Alosterna tabacicolor* (Degeer, 1775), *Anastrangalia dubia* (Scopoli, 1763), *Stictoleptura scutellata* (Fabricius, 1781), *Stictoleptura maculicornis* (Degeer, 1775), *Stictoleptura rubra* (Linnaeus, 1758), *Rutpela maculata* (Poda, 1761), *Leptura quadrifasciata* Linnaeus, 1758, *Stenurella melanura* (Linnaeus, 1758)

Prioninae: *Prionus coriarius* (Linnaeus, 1758)

Spondylidinae + Aseminae: *Spondylis buprestoides* (Linnaeus, 1758), *Asemum striatum* (Linnaeus, 1758), *Arhopalus rusticus* (Linnaeus, 1758), *Tetropium castaneum* (Linnaeus, 1758)

Chrysomelidae

Chrysomelinae: *Timarcha tenebricosa* (Fabricius, 1775)

Donaciinae: *Donacia vulgaris* Zschach, 1788

Orsodacninae: *Orsodacne cerasi* (Linnaeus, 1758)

In addition, many drawings from the literature were examined in order to reach a wider basis for comparison. Illustrations of male genitalia of the following taxa were included in our analysis:

Cerambycidae

Anoplodermatinae – 5 taxa (DIAS 1984, 1986, 1987)

Cerambycinae – 27 taxa (BAHILLO DE LA PUEBLA & ITURRONDOBEITIA 1996; FRAGOSO 1985a; FRANCESCHINI 2002; IUGA & ROSCA 1961; KUMAR & VERMA 1980; MONNÉ & NAPP 2000; MOURA & GALILEO 1992; NIISATO 1987; SHARP & MUIR 1912; WANG 1995; WU & JIANG 1993; ZIA 1936)

Lamiinae – 53 taxa (BAHILLO DE LA PUEBLA & ITURRONDOBEITIA 1996; BENSE 1995; BREUNING & TEOCCHI 1977; IUGA & ROSCA 1961; JULIO 1999; MARTINS & GALILEO 1998; SAMA 1988; SHARP & MUIR 1912; TSHERNYSHEV & DUBATOLOV 2000; TYSON 1973; VERDUGO PAEZ 1994; WU & JIANG 1989; ZIA 1936)

Lepturinae – 22 taxa (BAHILLO DE LA PUEBLA & ITURRONDOBEITIA 1996; BENSE 1995; DEVESA REGUEIRO & BAHILLO DE LA PUEBLA 2003; IUGA & ROSCA 1961; KINEL 1931; OHBAYASHI 1970; VILLIERS 1982)

Oxypeltinae – 2 taxa (FRAGOSO 1985b)

Parandrinae – 1 taxon (GILBERT 1952)

Philinae – 6 taxa (WU & JIANG 2000)

Prioninae – 73 taxa (IUGA & ROSCA 1961; QUENTIN & SIMONETTA 1992; QUENTIN & VILLIERS 1977, 1978, 1981, 1983; ZIA 1936)

Spondylidinae + Aseminae – 2 taxa (BAHILLO DE LA PUEBLA 1991)

Vesperinae – 2 taxa (BENSE 1995)

Chrysomelidae

Aulacoscelidinae – 4 taxa (JOLIVET 1957; SUZUKI 1994)

Bruchidae – 10 taxa (KINGSOLVER 1970; SCHMITT 1985a; TERAN & MURUA DE L'ARGENTIER 1981; ZIA 1936)

Chrysomelinae (*Timarcha*) – 4 taxa (IABLOKOFF-KHNZORIAN 1966; JOLIVET 1957; POWELL 1941; SHARP & MUIR 1912)

Donaciinae – 8 taxa (HARNISCH 1915; IABLOKOFF-KHNZORIAN 1966; POWELL 1941; SCHMITT 1985a, 1985b; SHARP & MUIR 1912; ZIA 1936)

Megalopodinae – 3 taxa (JOLIVET 1957; ZIA 1936)

Orsodacninae – 1 taxon (POWELL 1941)

Palophaginae – 2 taxa (KUSCHEL & MAY 1990)

Sagrinae – 18 taxa (JOLIVET 1957; MANN & CROWSON 1991; SCHMITT 1985b; ZIA 1936)

Zeugophorinae – 2 taxa (CHUJO 1952; IABLOKOFF-KHNZORIAN 1966)

In total the parameres of 216 taxa of Cerambycidae and 55 taxa of Chrysomelidae have been compared.

Genitalia were dissected using forceps and insect pins under a WILD M3 Z stereoscope. The genitalia were placed in 80% ethanol for 20 min and then in 100% ethanol until dissection. Finally, they were treated with ultrasound to complete the cleaning process.

In preparation for scanning electron microscopy, the air-dried genitalia were coated with gold in an ANATECH HUMMER VII and examined with an HITACHI S-2460 N (SEM).

3. RESULTS

3.1. Characters of the parameres

The first character we examined was the degree of sclerotization of the aedeagus, including the tegmen which varies from extreme, with nearly black pigmentation in lepturine beetles of the genera *Leptura, Stictoleptura, Rutpela* and *Stenurella* and in *Agapanthia* (Lamiinae) to weak with light yellow in other lepturine genera (*Alosterna, Carilia, Dinoptera, Grammoptera*). Most of the long-horned species studied have reddish-brown aedeagi, representing a medium sclerotized state. In chrysomelids, the species studied have poor to medium degrees of sclerotization of their aedeagi with light yellow to brown colours.

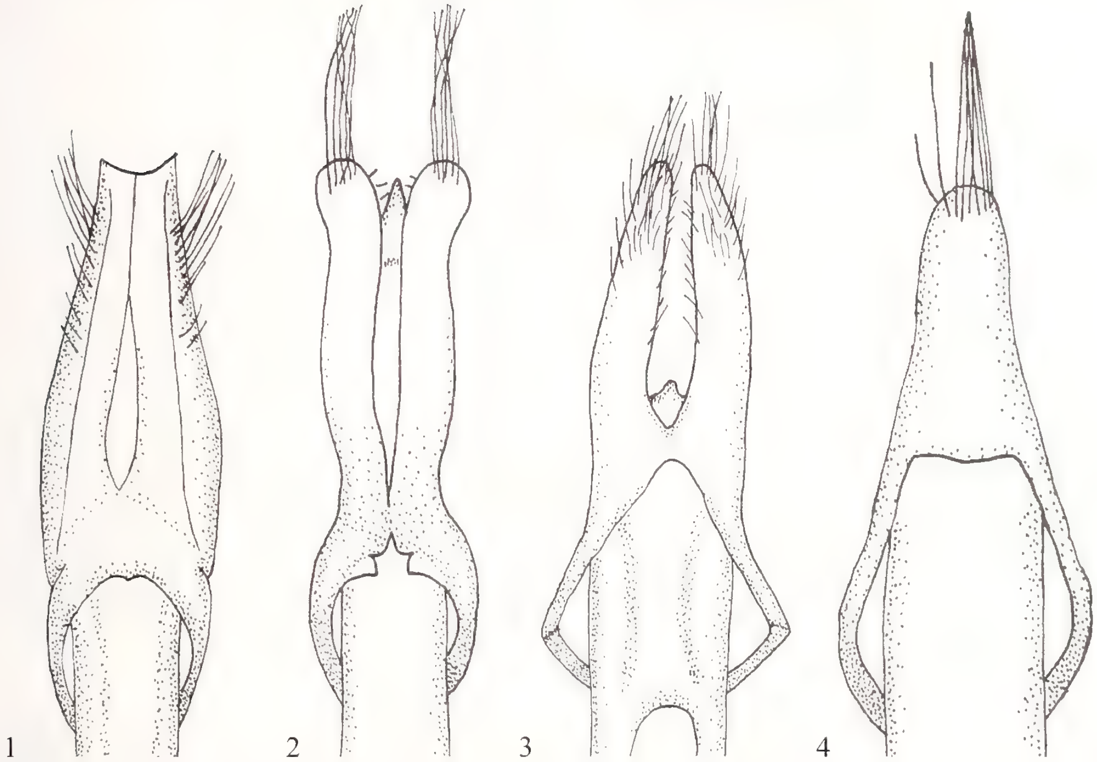


Fig. 1-4. Parameres of *Rutpela maculata* (1), *Leptura quadrifasciata* (2), *Spondylis buprestoides* (3), and *Obrium brunneum* (4).

The second character we measured was the relative paramere length, which is herein referred to only as the non-fused portion of each paramere or lobe. The paramere width was measured at the mid point of the non-fused portion to its lateral extension and then was related to the overall length of the lobes. Sometimes there is no division of the parameres if they are fused together (Fig. 4). In other cases the parameres are divided, very long and slender (Fig. 2). Within some subfamilies of Cerambycidae, it is possible to separate some genera from others with the help of this character. There is only one known genus in the Cerambycidae (*Stenhomalus*) without parameres (WU & JIANG 1993). Within the taxa of this family studied, only some genera of Cerambycinae (*Callimellum, Hybodera, Obrium, Skeletodes* and *Stenopterus*) and the Oxypeltinae – altogether only 5 % of the cerambycid taxa studied so far – show totally fused parameres. Within Chrysomelidae, the parameres in Donaciinae, *Timarcha*, Zeugophorinae and some Bruchidae are fused, but in the other groups, like Orsodacninae, Sagrinae and most Bruchidae, they are divided. Parameres are fused in 34 % of the paramere-possessing chrysomelid taxa we studied. However, even in the chrysomelid groups with non-fused parameres, these structures are comparatively short. The mean relative length of all taxa with non-fused parameres is 3.2 in

Cerambycidae (standard deviation =1.4; n=194) and 1.6 in Chrysomelidae (standard deviation = 0.9; n=34). Only two of the chrysomelids (both from Aulacoscelidinae) have parameres with a relative length of 4, all other taxa 1 to 3. In both families, Cerambycidae and Chrysomelidae, there are taxa with exceptionally long and slender parameres, which were not considered in calculating the mean values, because they would have disturbed the other data: The Madagascan Lepturinae of the genus *Mastododera* and related genera (VILLIERS 1982) with a relative length of 13 (other cerambycids not higher as 7) and an undetermined *Bruchus* (ZIA 1936) with a relative length of 32 (other chrysomelids not higher as 4).

The third character we considered was the orientation of the lobes, or the direction of the apex. They can be shaped like an arrow (Fig. 3), V-shaped (Fig. 2) or cling tightly next to each other (Fig. 1). Most cerambycids have converging lateral lobes, but most subfamilies show two or three conditions. Among chrysomelids with non-fused parameres, only most Sagrinae and some Bruchidae have divergent parameres. Only one species of Sagrinae has parameres which stretch out parallel. All Megalopodinae, Palophaginae, Aulacoscelidinae and Orsodacninae studied have converging parameres.

Additionally, the apex of the parameric lobes can look ragged or cut (Fig. 1), pointed (Fig. 3) or broadly rounded (Fig. 2). Most cerambycid parameres are pointed, but at least in Lepturinae, there are also some species with ragged and broadly rounded lateral lobes. Chrysomelid beetles show in addition to pointed apices of lateral lobes, protracted parameres (in Orsodacninae).

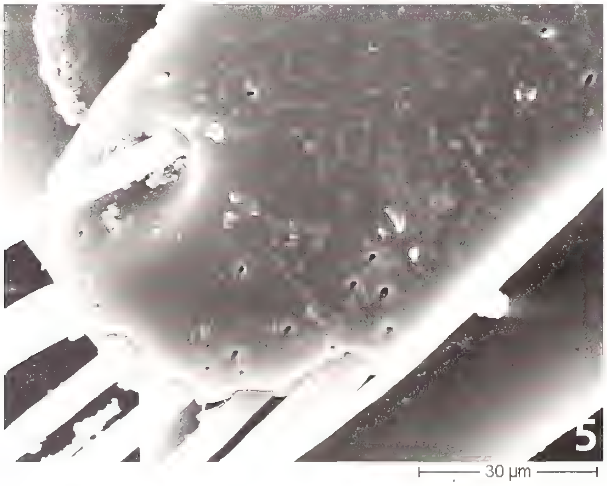
Hubweber (unpubl. data) divided the number and density of setae on the parameres into three different characters, according to their position (apical, ventral and dorsa-lateral). Probably the best character of these is the number and density of dorsa-lateral setae. All studied species of Lepturinae (Cerambycidae) lack setae at this region (Fig. 2), except one species with a few sparse setae (Fig. 1), while all species of the other long-horn subfamilies studied possess setae dorsalaterally (Fig. 3). On the other hand, ventral setae are widely variable, even between very closely related groups. The leaf beetle species examined possess long setae at the apex of the parameres, but only a few taxa are known with dorsalateral or ventral setae.

The tegminal ring can either be narrow (Fig. 2) or wide (Fig. 3). "Wide" means that the lateral gap between the ring and median lobe is at least as wide as the ring itself. In cerambycid beetles, most lepturine species have a narrow tegminal ring, while most (but not all) species of the other subfamilies have a broad ring. In Cerambycids, 39 % of the taxa studied (n=37) have a wide tegminal ring, while only 19 % of chrysomelid taxa studied (n=26) show this condition.

Additionally, the connection of between the parameres and the basal piece is either angular (Fig. 3) or rounded (Fig. 2). It is not easy to distinguish between "angled" or "rounded", consequently if there is a sudden bend we call it "angled". In the longicorn beetles studied (n=68), 44 % show the angled condition, while only 7 % or two species, *Amblycerus robiniae* (KINGSOLVER 1970) and *Orsodacne cerasi* (own observation), of the leaf beetles studied (n=26) show this condition.

3.2. Presumed glandular openings

A recent discovery is tiny holes near the apex of the parameres of *Donacia* (Fig. 5). We suggest that these are most probably not sensilla, because they do not contain traces of setae. Similar, but not so many holes are found on the parameres of *Prionus* (Fig. 6), *Stenopterus* and *Zeugophora*. In *Alosterna* none such holes are found on the parameres.



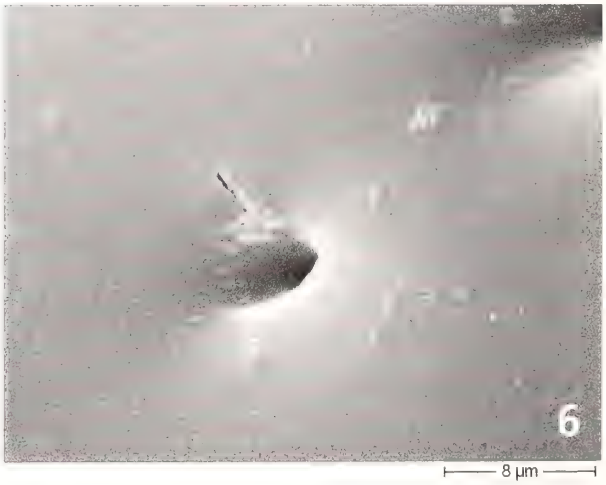


Fig. 5–6. (5) Apex of the paramere of *Donacia vulgaris* with tiny holes, (6) Tiny hole on paramere of *Prionus coriarius*.

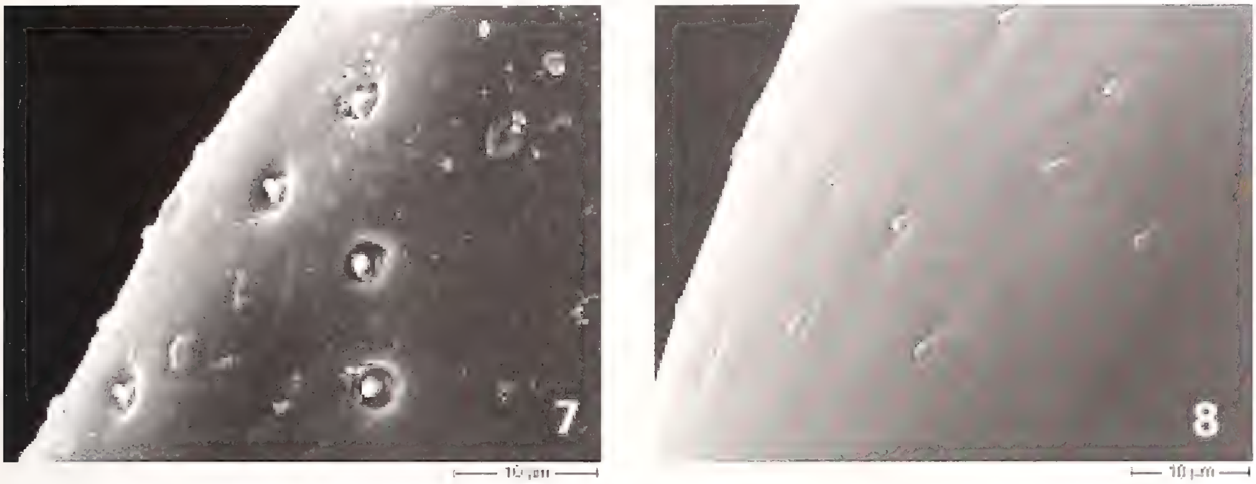


Fig. 7–8. (7) Sensilla on the median lobe of *Donacia vulgaris*, (8) Sensilla on the apex of the median lobe of *Orsodacne cerasi*.

HAMMOND (1972) described true, peg-liked setae of unknown function on the parameres of Staphylinidae. In contrast to the holes on the parameres, sensilla with a minute seta can be found along the inner margin of the median lobe in *Donacia* and *Orsodacne* (Figs. 7 and 8). These campaniform sensilla look similar as those observed on the median lobe of Platypodidae (EPILA-OTARA & TRIPLEHORN 1990).

4. DISCUSSION

We suggest that the sclerotization in Cerambycidae is thicker than in Chrysomelidae generally, because of thicker sclerotization of the female vaginal tract. Many species of long-horned beetles lay their eggs just beneath the bark of trees and presumably a more stout or heavily sclerotized ovipositor is required and – possibly – a more thickly sclerotized aedeagus, too.

The mean value of the relative length of the lateral lobes through 194 cerambycid species is 3.2. We know only a few chrysomelid species from our own investigations or from drawings in the literature with a relative length greater than 3. Of course, there is one subfamily among Chrysomelidae with long and narrow parameres, the Donaciinae, but these parameres are fused. We can also summarise that the parameres of Cerambycidae are generally more deeply divided than those of Chrysomelidae.

Obviously, the parameres of Chrysomelidae bear less dorsolateral and ventral setae than Cerambycidae. We have no proper explanation for this observation. However, if KINGSOLVER's (1970) hypothesis holds true – that parameres outside the female genital tract are used to position the male genitalia – then it may be that the setae on the parameres perform a sensorial function. For example they could sense the position of the median lobe inside the female or press on the sternites of the female to facilitate the release of sperm to the proper regions inside the female.

What is the function of the tiny holes on the parameres? One possibility is that they serve as glandular openings, but what could they secrete? Striking is the fact that they are more numerous on the parameres of *Donacia*, a beetle with a semi-aquatic mode of life. Therefore it may be they secrete a hydrophobic substance.

One question remains: Why are parameres divided in most of the groups studied, but undivided or totally reduced in some chrysomelids and in some Cerambycinae like *Obrium* and *Stenhomalus*? Possibly the function of these two states is quite different, for example the undivided condition serves like a lever in Donaciinae, as described by HARNISCH (1915) and in divided parameres they are sensory, as suggested by DÜNGELHOEF & SCHMITT (2006), or stimulatory, as assumed by EBERHARD (1985), and others. CROWSON & CROWSON (1996) suggested that the parameres have been reduced in some groups because of the problems of copulation on an unstable leaf surface. However, nearly all cerambycid beetles have parameres and many of them copulate on an unstable flower or leaf surface.

Future studies should include a comprehensive comparison of paramere morphology in more closely related cerambycids and chrysomelids. Because the taxa studied may not be representative, or taxa with especially noticeable parameres could have been overlooked in this study, we recommend selecting paired groups of sister taxon. In addition, live beetles in copula should be observed to solve the riddle of the parameres' function. In particular, the function of the tegmen in the closely related genera of *Obrium* and *Stenhomalus* could prove very interesting because of the obvious reduction and loss of parameres in these groups. The Madagascan species of Lepturinae and the bruchid species also have interesting morphologies with very long and narrow parameres. Histological and TEM-studies should clarify the structure of the tiny holes found on the apex of the parameres.

Acknowledgements. We thank Susanne Düngelhoef (ZFMK, Bonn) for discussion on the question of functional morphology of the parameres and two anonymous referees for helping to improve our manuscript. Bradley Sinclair (ZFMK, Bonn) kindly checked the manuscript for language corrections. Lasse Hubweber is grateful for funding of his doctoral studies by the Cusanuswerk.

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Bonner zoologische Beiträge	Band 54 (2005)	Heft 4	Seiten 261–269	Bonn, Oktober 2006

Leaf Beetles (Insecta: Coleoptera: Chrysomelidae) Suffer From Feeding on Fern Leaves[1]

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Abstract. Two age groups of larvae of *Agelastica alni* (Linnaeus, 1758) and *Phratora vitellinae* (Linnaeus, 1758) were provided with treated or untreated leaves of their actual host plant (*Alnus glutinosa* or *Salix spp.*, respectively) or of the ferns *Athyrium filix-femina*, *Dryopteris austriaca* and *D. filix-mas*. "Treated" leaves were covered with an aqueous extract of host plant or fern leaves. Mortality of young larvae (one-day old) of *A. alni* was significantly higher when provided with treated or untreated fern leaves and treated food plant leaves compared to untreated food plant leaves. Mortality of older larvae (six-day old) was significantly lower than that of young larvae. Young larvae did not feed on fern leaves at all, while older larvae ingested material from treated fern leaves, however at low rates. *Phratora vitellinae* individuals showed abnormal elytra and irregular melanisation patterns when they had taken up fern substances. In both species, the larvae produced less defensive secretion if they had ingested an extract of *Athyrium filix-femina.*

Key words. *Agelastica alni*, *Phratora vitellinae*, Filicatae: Aspidiaceae, phytophagy, larval development

1. INTRODUCTION

There are 12,500 species of ferns and 230,500 species of seed plants (SPECK 1992). Some 140,000 species of Phytophaga (= Pseudotetramera = Curculionoidea + Cerambycidae + Bruchidae + Chrysomelidae; Lexikon der Biologie, Urania-Tierreich) mean a proportion of one species of pseudotetramerous beetles per 1.7 species of spermatophyte plant, but only 105 species of Phytophaga are known to feed on ferns (BALICK et al. 1978), producing a proportion of 1:119.0. According to HENDRIX (1980) of 726,000 species of insects known at that time, 338,000 are phytophagous (1:0.7), but only 465 feed on ferns (1:26.9). Of the 413 arthropod species reported as found on ferns, 93 attack bracken (*Pteridium aquilinum*) exclusively, making the proportion 1:33.3. Even if these numbers must be corrected for uneven numbers of individuals or/and different availability of biomass, it is clear that there are much less leaf beetles (Chrysomelidae) feeding on ferns than could be expected according to species numbers. There might be regional exceptions (e.g., Veracruz, Mexico: BALICK et el. 1978; Hawaii: SWEZEY 1922). Especially arthropods with chewing mouthparts are remarkably underrepresented on ferns as compared to the large percentage of insects with sucking mouthparts (Thysanoptera, Heteroptera, Homoptera; HENDRIX 1980; HILL 1998; D'ROZARIO & BERA 2003).

Data from bracken (e.g., MARTINS et al. 1995; GILMAN & COOPER-DRIVER 1998) can be generalised only with care since this fern species is (1) certainly the most abundant fern species on earth, and (2) is regarded a pest since it causes illness to cattle when fed. Thus, bracken is definitively the most intensively studied fern species.

In other taxa, for example, Lithinine moths, there might have been a phylogenetic adaptation towards fern feeding (WEINTRAUB et al. 1995). The sawfly *Strongylogaster osmundae* (Takeuchi, 1941) (Hymenoptera: Tenthredinidae) develops obligatorily on the osmund fern, *Osmunda japonica*. In leaf beetles, however, there is no indication that any species is especially adapted to the exploitation of this food resource. For example, WINTERBOURN (1987) found beetles of seven families on bracken, amongst them no leaf beetles, a result also supported by MESIBOV (2001). MUKHOPADHYAY & THAPA (1994) list 19 beetle species, among them seven species of Chrysomelidae as "associated with ferns", however without providing any information as to the intensity of this "association". Since among the seven leaf beetles listed by MUKHOPADHYAY & THAPA there is also *Aspidimorpha sanctaecrucis* (Fabricius, 1792), which is definitely restricted to Convulvulaceae (GHATE et al. 2003), one should draw conclusions very cautiously. Possible reasons for the strikingly lower number of phytophagous beetles on ferns than on angiosperms could be that ferns are either toxic, or have repellents, or lack attractants.

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[1] Paper presented to the 6th International Symposium on the Chrysomelidae, Bonn, Germany, May 7, 2004.

In order to shed some light on these questions for three species of Central European ferns (*Athyrium filix-femina* (Lady Fern), *Dryopteris austriaca* (Wood Fern) and *D. filix-mas* (Male Fern), we conducted feeding experiments with two species of leaf beetles, *Agelastica alni* (Linnaeus, 1758) and *Phratora vitellinae* (Linnaeus, 1758).

2. MATERIALS AND METHODS

Fifteen adult individuals of *Agelastica alni* were collected from Common Alder (*Alnus glutinosa*) in the surroundings of Freiburg im Breisgau, Germany. They were kept in plastic containers on a layer of gypsum and fed with fresh alder leaves. Their eggs were collected and the hatched larvae were fed on fresh leaves of their original food plant until they were used in the tests. We conducted two series of tests: (1) with "young" – i.e., freshly hatched – larvae, and (2) with "old" – i.e., six-day old – larvae. In both age groups feeding traces and mortality were registered on day 3, 8, and 10 after the beginning of the experiment.

Adults of *Phratora vitellinae* were collected from willows and poplars growing in a park area on the outskirts of Freiburg im Breisgau. They were kept and treated as the individuals of *Agelastica alni*. However, since considerably less larvae of *Phratora vitellinae* could be obtained, meaningful statistical analysis was not possible.

Leaves of *Athyrium filix-femina*, *Dryopteris austriaca* and *D. filix-mas* were collected in a forest close to the city of Freiburg im Breisgau ("Sternwald"), always from the same area. Aqueous extracts were made from fresh leaves and from those dried for four weeks at room temperature. The leaves were put into tab water for 30 minutes and then squeezed with broad forceps in order to gain not only water-soluble but also lipophilous substances. The test leaves were soaked with the respective extracts for 30 minutes in order to mask their contact chemical properties.

Table 1. Experimental Settings

Test Number	Kind of Food Offered
1	Normal food plant (f.p.) masked with extract from dried *Dryopteris filix-mas (D.f.)*
2	Normal food plant (f.p.) masked with extract from dried *Dryopteris ausriaca (D.a.)*
3	Normal food plant (f.p.) masked with extract from dried *Athyrium filix-femina (A.f.)*
4	Dried *D. filix-mas* masked with extract from the normal food plant
5	Dried *D. austriaca* masked with extract from the normal food plant
6	Dried *A. filix-femina* masked with extract from the normal food plant
7	Dried *D. filix-mas*, swelled in tab water
8	Dried *D. austriaca*, swelled in tab water
9	Dried *A. filix-femina*, swelled in tab water
10	Dried normal food plant, swelled in tab water
11	Normal food plant masked with extract from fresh *Dryopteris filix-mas*
12	Normal food plant masked with extract from fresh *Dryopteris ausriaca*
13	Normal food plant masked with extract from fresh *Athyrium filix-femina*
14	Fresh *D. filix-mas* masked with extract from the normal food plant
15	Fresh *D. austriaca* masked with extract from the normal food plant
16	Fresh *A. filix-femina* masked with extract from the normal food plant
17	Fresh *D. filix-mas*, swelled in tab water
18	Fresh *D. austriaca*, swelled in tab water
19	Fresh *A. filix-femina*, swelled in tab water
20	Fresh normal food plant, swelled in tab water
21	Fresh *D. filix-mas*, untreated
22	Fresh *D. austriaca*, untreated
23	Fresh *A. filix-femina*, untreated
24	Fresh normal food plant, untreated

For each of the two test series 24 setups were designed. The details are given in Table 1. The test larvae were kept under the described conditions until either all were dead or the first individuals tried to pupate (which can easily be recognised as *Agelastica alni* beetles pupate in the soil. Thus, larvae ready to pupate attempt at digging holes in the gypsum). *Phratora vitellinae* pupate on the leaves of their food plant, the initiation of their pupation can be observed directly.

We used the Statistical Package for Social Sciences (SPSS) to calculate a logistic regression. Probabilities of error were calculated by Chi^2 or Fisher's exact test (the latter in cases where n was too low for Chi^2).

Table 2. Mortality rates of *Agelastica alni* under test conditions. ■ : traces of feeding on leaves on all test days, □ : no traces of feeding on any test day, ▣ : traces of feeding on some test days only (and to a considerably less degree). *A.f.: Athyrium filix-femina; D.a: Dryopteris austriaca; D.f.: Dryopteris filix-mas;* f.p.: normal food plant (*Alnus glutinosa*)

		Young larvae				Old larvae		
Test No.			**Day 3 alive/dead**	**Day 8 alive/dead**	**Day 10 alive/dead**		**Day 3 alive/dead**	**Day 8 alive/dead**	**Day 10 alive/dead**
1	(F.p. masked with dried *D.f.*)	■	18/1	12/7	10/9	■	16/10	13/2	12/2
2	(F.p. masked with dried *D.a.*)	■	17/2	14/5	14/5	■	17/1	13/4	13/4
3	(F.p. masked with dried *A.f.*)	■	17/2	6/12	5/13	■	16/1	14/3	13/4
4	(Dried *D.f.* masked with f.p.)	□	1/16			▣[3]	20/1	0/21	
5	(Dried *D.a.* masked with f.p.)	□	19/2			▣[3]	19/1	0/20	
6	(Dried *A.f.* masked with f.p.)	□	14/4			▣[3]	18/0	0/18	
7	(Dried *D.f.* swelled)	▣[2]	12/7	0/19		▣[4]	18/2		
8	(Dried *D.a.* swelled)	□	4/17			▣[4]	19/1		
9	(Dried *A.f.* swelled)	□	9/8			▣[4]	20/0		
10	(Dried f.p. swelled)	▣[1]	19/1	2/17	0/19	■	22/0	18/4	17/5
11	(F.p. masked with fresh *D.f.*)	■	20/0	19/0	19/0	■	19/1	17/3	17/3
12	(F.p. masked with fresh *D.a.*)	■	19/1	16/3	15/4	■	17/3	17/3	17/3
13	(F.p. masked with fresh *A.f.*)	■	20/0	17/2	17/2	■	19/0	17/2	17/2
14	(Fresh *D.f.* masked with f.p.)	□	0/20			▣[5]	11/19	0/30	
15	(Fresh *D.a.* masked with f.p.)	□	0/20			▣[6]	17/2	0/19	
16	(Fresh *A.f.* masked with f.p.)	□	4/16			▣[7]	17/0	0/17	
17	(Fresh *D.f.* swelled)	□	0/18			□	12/15		
18	(Fresh *D.a.* swelled)	□	0/20			□	20/0		
19	(Fresh *A.f.* swelled)	□	0/12			□	19/1		
20	(Fresh f.p. swelled)	■	19/0	17/1	15/3	■	20/0	20/0	20/0
21	(Fresh *D.f.* untreated)	▣[2]	9/14	0/23		□	13/2		
22	(Fresh *D.a.* untreated)	□	3/15			□	7/8		
23	(Fresh *A.f.* untreated)	□	12/0			□	10/15		
24	(Fresh f.p. untreated)	■	83/0	80/0	79/0	■	79/0	74/5	74/5

[1]: Up to day 7 less feeding traces per day, from day 7 through day 10 no more feeding traces at all.
[2]: Up to day 3 less feeding traces per day, after day 4 no more live larvae.
[3]: Up to day 3 very few feeding traces per day, after day 3 no more traces, no live larvae from day 5.
[4]: Few feeding traces on day 1, thereafter no more traces.
[5]: Up to day 3 few feeding traces, after day 3 no more live larvae
[6]: Few feeding traces on day 1, thereafter no more traces, no more live larvae after day 4.
[7]: Only on days 2 and 3 traces of feeding, no more live larvae after day 4.

3. RESULTS

3.1. *Agelastica alni*

The results of the feeding experiments are listed in Table 2. Decreasing total numbers of individuals are due to the fact that some larvae managed to escape from the test boxes. The nearly non-existing mortality in the control sample proves that the experimental conditions were appropriate. In addition to the observed numerical results we found that those larvae who had taken up extract from dried or fresh *Athyrium filix-femina* produced conspicuously less defensive secretion when disturbed than those larvae fed on untreated normal food plant or on normal food plant masked with extract of the other two fern species. Moreover, duration of larval stage 2 lasted for 12 days when the larvae were fed on normal food plant masked with extract from dried *Athyrium filix-femina* as compared to nine days in the control group, or 8.5 to 10 days in the other tests with normal but treated food plant.

The logistic regression revealed a significant influence of food (which plant matter was offered) and the masking of the test food (with the exception of *Dryopteris felix-mas*, the extract of which had no significant influence), whereas the treatment of the test food and of the masking (dried and swelled or fresh) did not lead to significant differences.

In Table 3 we present the results of comparisons between different experimental settings, for young and old larvae. Due to the high mortality in some tests, only those data are presented completely where enough larvae survived up to day 10.

Table 3. Comparison of the mortality rates under different test conditions against control (test no. 24). Probabilities of error calculated with Chi^2 or Fisher's Exact

3a: Young larvae

Test No.		**Probability of Error**
1	(F.p. masked with dried *D.f.*) on day 10 > control	$p < 0.001$
2	(F.p. masked with dried *D.a.*) on day 10 > control	$p < 0.001$
3	(F.p. masked with dried *A.f.*) on day 10 > control	$p < 0.001$
4	(Dried *D.f.* masked with f.p.) on day 3 > control	$p < 0.001$
5	(Dried *D.a.* masked with f.p.) on day 3 > control	$p < 0.040$
6	(Dried *A.f.* masked with f.p.) on day 3 > control	$p < 0.001$
7	(Dried *D.f.* swelled) on day 3 > control	$p < 0.001$
8	(Dried *D.a.* swelled) on day 3 > control	$p < 0.001$
9	(Dried *A.f.* swelled) on day 3 > control	$p < 0.001$
10	(Dried f.p. swelled) on day 10 > control	$p < 0.001$
11	(F.p. masked with fresh *D.f.*) on day 10 > control	n.s.
12	(F.p. masked with fresh *D.a.*) on day 10 > control	$p < 0.002$
13	(F.p. masked with fresh *A.f.*) on day 10 > control	$p < 0.040$
14	(Fresh *D.f.* masked with f.p.) on day 3 > control	$p < 0.001$
15	(Fresh *D.a.* masked with f.p.) on day 3 > control	$p < 0.001$
16	(Fresh *A.f.* masked with f.p.) on day 3 > control	$p < 0.001$
17	(Fresh *D.f.* swelled) on day 3 > control	$p < 0.001$
18	(Fresh *D.a.* swelled) on day 3 > control	$p < 0.001$
19	(Fresh *A.f.* swelled) on day 3 > control	$p < 0.001$
20	(Fresh f.p. swelled)	no difference to control
21	(Fresh *D.f.* untreated) on day 3 > control	$p < 0.001$
22	(Fresh *D.a.* untreated) on day 3 > contro	$p < 0.001$
23	(Fresh *A.f.* untreated) on day 3 > control	n.s.

3b: Old larvae

Test No.		Probability of Error
1,2,3	1 (f.p. masked with dried *D.f.*), 2 (f.p. masked with dried *D.a.*, 3 (f.p. masked with dried *A.f.*) on day 10	no differences to control
4,5,6	4 (Dried *D.f.* masked with f.p.), 5 (Dried *D.a.* masked with f.p.), 6 (Dried *A.f.* masked with f.p.) on day 3	no differences to control
7	(Dried *D.f.* swelled) on day 3 > control	$p < 0.040$
8	(Dried *D.a.* swelled), 9 (Dried *A.f.* swelled) on day 3	no differences to control
10	(Dried f.p. swelled) on day 10 > control	$p < 0.040$
11	(F.p. masked with fresh *D.f.*), 12 (F.p. masked with fresh *D.a.*), 13 (F.p. masked with fresh *A.f.*) on day 10:	no differences to control
14	(Fresh *D.f.* masked with f.p.) on day 3 > control	$p < 0.001$
15	(Fresh *D.a.* masked with f.p.) on day 3 > control	$p < 0.040$
16	(Fresh *A.f.* masked with f.p.) on day 3 > control	n.s.
17	(Fresh *D.f.* swelled) on day 3 > control	$p < 0.001$
18	(Fresh *D.a.* swelled), 19 (Fresh *A.f.* swelled) on day 3:	no differences to control
20	(Fresh f.p. swelled) on day 10 > control	n.s.
21	(Fresh *D.f.* untreated) on day 3 > control	$p < 0.030$
22	(Fresh *D.a.* untreated) on day 3 > control	$p < 0.001$
23	(Fresh *A.f.* untreated) on day 3 > control	$p < 0.001$

Table 4. Comparison of the mortality rates of young and old larvae under different test conditions. Probabilities of error calculated with Chi^2 or Fisher's Exact

Test No.		Probability of Error
1	(F.p. masked with dried *D.f.*) young > old on day 10	$p < 0.050$
2	(F.p. masked with dried *D.a.*) young > old on day 10	n.s.
3	(F.p. masked with dried *A.f.*) young > old on day 10	$p < 0.010$
4	(Dried *D.f.* masked with f.p.) young > old on day 3	$p < 0.010$
5	(Dried *D.a.* masked with f.p.) young > old on day 3	n.s.
6	(Dried *A.f.* masked with f.p.) young > old on day 3	n.s.
7	(Dried *D.f.* swelled) young > old on day 3	$p < 0.050$
8	(Dried *D.a.* swelled) young > old on day 3	$p < 0.001$
9	(Dried *A.f.* swelled) young > old on day 3	$p < 0.002$
10	(Dried f.p. swelled) young > old on day 10	$p < 0.010$
11	(F.p. masked with fresh *D.f.*)	no difference between young and old on day 10
12	(F.p. masked with fresh *D.a.*)	no difference between young and old on day 10
13	(F.p. masked with fresh *A.f.*)	no difference between young and old on day 10
14	(Fresh *D.f.* masked with f.p.) young > old on day 3	$p < 0.001$
15	(Fresh *D.a.* masked with f.p.) young > old on day 3	$p < 0.001$
16	(Fresh *A.f.* masked with f.p.) young > old on day 3	$p < 0.001$
17	(Fresh *D.f.* swelled) young > old on day 3	$p < 0.001$
18	(Fresh *D.a.* swelled) young > old on day 3	$p < 0.001$
19	(Fresh *A.f.* swelled) young > old on day 3	$p < 0.001$
20	(Fresh f.p. swelled) young > old on day 10	n.s.
21	(Fresh *D.f.* untreated) young > old on day 3	$p < 0.010$
22	(Fresh *D.a.* untreated) young > old on day 3	n.s.
23	(Fresh *A.f.* untreated) young > old on day 3	n.s.
24	(Fresh f.p. untreated) young > old on day 10	$p < 0.030$

Table 5. Comparison of mortality rates on the three fern species. Probabilities of error calculated with Chi² or Fisher's Exact

5a: Young larvae

Test No.		Probability of Error
1	(F.p. masked with dried *D.f.*) > 2 (F.p. masked with dried *D.a.*) on day 10	n.s.
3	(F.p. masked with dried *A.f.*) > 1 (F.p. masked with dried *D.f.*) on day 10	n.s.
3	(F.p. masked with dried *A.f.*) > 2 (F.p. masked with dried *D.a.*) on day 10	n.s.
4	(Dried *D.f.* masked with f.p.) > 5 (Dried *D.a.* masked with f.p.) on day 3	$p < 0.001$
4	(Dried *D.f.* masked with f.p.) > 6 (Dried *A.f.* masked with f.p.) on day 3	$p < 0.001$
6	(Dried *A.f.* masked with f.p.) > 5 (Dried *D.a.* masked with f.p.) on day 3	n.s.
8	(Dried *D.a.* swelled) > 7 (Dried *D.f.* swelled) on day 3	$p < 0.010$
9	(Dried *A.f.* swelled) > 7 (Dried *D.f.* swelled) on day 3	$p > 0.050$
8	(Dried *D.a.* swelled) > 9 (Dried *A.f.* swelled) on day 3	$p < 0.050$
22	(Fresh *D.a.* untreated) > 21 (Fresh *D.f.* untreated) on day 3	n.s.
21	(Fresh *D.f.* untreated) > 23 (Fresh *A.f.* untreated) on day 3	$p < 0.001$
22	(Fresh *D.a.* untreated) > 23 (Fresh *A.f.* untreated) on day 3	$p < 0.001$

5b: Old larvae

Test No.		Probability of Error
1	(F.p. masked with dried *D.f.*) > 2 (F.p. masked with dried *D.a.*) on day 10	n.s.
3	(F.p. masked with dried *A.f.*) > 1 (F.p. masked with dried *D.f.*) on day 10	n.s.
3	(F.p. masked with dried *A.f.*) > 2 (F.p. masked with dried *D.a.*) on day 10	$p < 0.050$
5	(Dried *D.a.* masked with f.p.) > 4 (Dried *D.f.* masked with f.p.) on day 3	$p < 0.050$
4	(Dried *D.f.* masked with f.p.) > 6 (Dried *A.f.* masked with f.p.) on day 3	n.s.
5	(Dried *D.a.* masked with f.p.) > 6 (Dried *A.f.* masked with f.p.) on day 3	n.s.
14	(Fresh *D.f.* masked with f.p.) > 15 (Fresh *D.a.* masked with f.p.) on day 3	$p < 0.020$
14	(Fresh *D.f.* masked with f.p.) > 16 (Fresh *A.f.* masked with f.p.) on day 3	$p < 0.010$
15	(Fresh *D.a.* masked with f.p.) > 16 (Fresh *A.f.* masked with f.p.) on day 3	n.s.
17	(Fresh *D.f.* swelled) > 18 (Fresh *D.a.* swelled) on day 3	$p < 0.001$
17	(Fresh *D.f.* swelled) > 19 (Fresh *A.f.* swelled) on day 3	$p < 0.001$
19	(Fresh *A.f.* swelled) > 18 (Fresh *D.a.* swelled) on day 3	n.s.
22	(Fresh *D.a.* untreated) > 21 (Fresh *D.f.* untreated) on day 3	$p < 0.050$
22	(Fresh *D.a.* untreated) > 23 (Fresh *A.f.* untreated) on day 3	n.s.
23	(Fresh *A.f.* untreated) > 21 (Fresh *D.f.* untreated) on day 3	n.s.

Comparisons of mortality of young and old larvae are given in Table 4. In some tests, it did not differ significantly, as long as only numbers of surviving larvae are counted. It was, however, evident that young larvae died more frequently from starvation because they refused to feed on certain food at all. Old larvae took up leaf matter in several tests but died afterwards, either due to intoxication or from starvation after refusal of further feeding.

There was no significant difference in mortality rates when tests with dried against fresh fern leaves were compared. Mortality was significantly higher on dried as compared to fresh food plant, and on normal food plant masked with extract from dried as compared to fresh *Dryopteris filix-mas* and *Athyrium filix-femina*.

In order to reveal possible differences between the three fern species, the respective settings have been compared. The results are given in Table 5. All comparisons not listed in Table 5 did not yield significant differences between the fern species.

3.2. *Phratora vitellinae*

As with *Agelastica alni*, those larvae who had taken up extract from dried or fresh *Athyrium filix-femina* produced conspicuously less defensive secretion when disturbed than those larvae fed on untreated normal food plant or on normal food plant masked with extract of the other two fern species. This applied especially to the first larval instar.

In addition, there occurred severe distortions of moulting, elytron formation and melanisation when the larvae were fed on willow leaves masked with extract from *Dryopteris filix-mas* (Fig. 1).

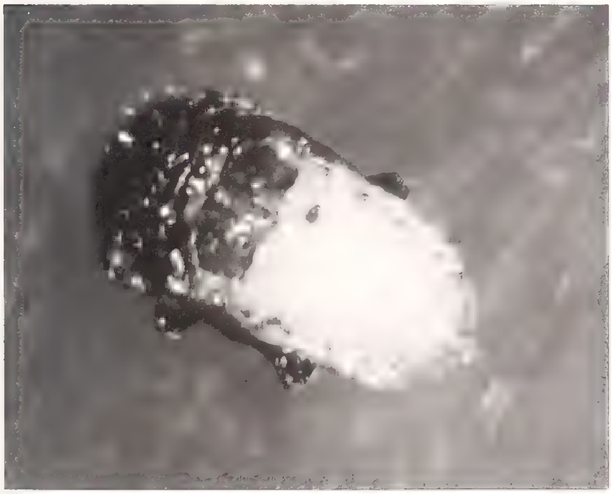

Fig. 1. Adult *Phratora vitellinae* showing massive wing deformation after having fed on willow leaves masked with extract of *Dryopteris-filix-mas*.

4. DISCUSSION

4.1. *Agelastica alni*

Young and old larvae fed on alder leaves even when they were covered with fern extract. This result is at odds with the generally held assumption that the foraging behaviour of herbivore insects is guided by olfactory and gustatory stimuli of the plants (e.g., DETHIER 1970; FRAENKEL 1959; HARBOURNE 1982; HSIAO 1969; SCHOONHOVEN 1972, 1973). JERMY (1966) stated that oligophagy is characterised rather by the avoidance of repellent substances than by search for attractants. This is rather unlikely since in our experiments the larvae avoided untreated fern leaves and accepted masked alder leaves as well as masked fern leaves which they should have despised according to JERMY'S statement. Obviously, feeding was triggered by the presence of feeding stimulants from alder leaves.

Mortality after feeding on alder leaves masked with extract from dry fern leaves demonstrates that at least toxic substances – and most probably also possible repellents and attractants – were in the aqueous extract at effective concentrations.

Of course, the mortality of young larvae fed on fresh or soaked fern leaves (see Table 4) could be caused by starvation. This definitively does not apply to the old larvae feeding on fern leaves masked with extract from leaves of the normal food plant (test nos. 4, 5, 6), who fed on leaves of all three fern species. The dramatic mortality (all test larvae were dead after five days) must be due to incompatible or toxic compounds.

The significantly higher mortality of old larvae in the control situation (test no. 24) is most probably due to the higher damage of the leaves they fed on as a consequence of their chewing. The partly damaged leaves dried faster than those the young larvae fed on.

Masking alder leaves with extract from fresh fern leaves (tests no. 11, 12, 13) did not lead to significant differences of mortality rates in young and old larvae. Thus, the extract cannot contain effective repellents and the toxic components of the extract do not affect young and old larvae to different extents. However, since in tests no. 12 & 13 with young larvae mortality was significantly higher than in the control, some substance in the aqueous extract of *Dryopteris austriaca* and *Athyrium filix-femina* must have had an effect on the young larvae.

The most interesting results are those of tests 14, 15, and 16 (fresh fern leaves masked with extract from normal food plant): young larvae did not feed on these leaves at all, old larvae ingested leaf material, on day 3 mortality was significantly higher on *Dryopteris filix-mas*, while after seven days no larva had survived. This is clear evidence that (1) some stimulus from the normal food plant caused the larvae to feed on fern leaves, and (2) that the ingestion of fern material causes death either by starvation or through toxic components. This explanation is supported by the results of tests no. 21, 22, and 23, where untreated fern leaves – with one exception – have not been ingested at all. In test no. 21, young larvae took up material of *D.f.*-leaves, however at decreasing amounts per day until on day 4 no larva had survived. This strange behaviour was most probably caused by two factors, in contrast to the other two fern species: the glandular trichomes are not exposed on the surface in *D.f.* and the larvae could, therefore, not that easily detect repellent or toxic substances from these glands, and young larvae possess probably less chemoreceptors than old ones. As SWAIN (1977) reports, the larvae of phytophagous insect are equipped with a lower number of chemoreceptors than adults. It seems plausible that the number of chemoreceptors increases during larval development. Since eggs are normally deposited on the larval food plant, and since first instar larvae are much less mobile than older ones, we can expect that young larvae are less choosy with respect to food plants than older ones.

4.2. *Phratora vitellinae*

Only a few larvae were available, so the results of the feeding experiments do not allow for statistical analyses. The obvious result that adult beetles from those larvae who ingested components of *Dryopterix filix-mas* showed elytral deformations points in the same direction as the results of *A. alni*: *D. filix-mas* either contains more or more toxic substances than the other two ferns tested, or these substances reach higher quantities in the aqueous extract.

The small sample size does not permit sound generalisations from these results. However, there is hardly any other explanation for the distorted moulting than that the aqueous extract of *D. filix-mas* contained effective amounts of phytoecdysone. This is surprising since the study of SELVARAJ et al. (2005) revealed that steroids were only in the chloroform and ethanol extracts and in the hexane fraction, but not in the aqueous fraction of *Pteridium aquilinum*.

4.3. Conclusions

The larvae in our experiments fed on ferns only if these leaves were covered with an aqueous extract of the original food plant, *Alnus glutinosa* or *Salix* spp., respectively (with the one mentioned exception of young *Agelastica alni* larvae ingesting – and dying – from untreated leaves of *Dryopteris filix-mas*. Whenever larvae took up fern leave material, they suffered conspicuously, by dying, by less production of defensive secretion, or by wing deformation during pupal development. This means that (1) phytoecdysones contained in the fern leaves are not effective as repellents but as toxins. They can, therefore, indeed act as defence against phytophagous insects, however not unless these insects have ingested leave material. Thus, both points of view apply – that phytoecdysteroids do not deter insects from feeding on a fern plant (JONES & FIRN 1978) and that phytoecdysones form an effective protection against attacks of phytophagous insects (e.g., RUSSELL 1977). (2) Feeding activity on a certain plant is most probably triggered by the presence of feeding stimulants rather than prevented by the presence of repellents. (3) The differences found between the effectiveness of *Dryopteris filix-mas* and the other two fern species provides a further caveat against uncritical generalisations of results from studies with bracken (*Pteridium aquilinum*), which dominate the literature on fern-insect interaction.

Acknowledgements. We thank Gabriele Uhl, Bonn, for her help with the statistics and for critically commenting on the manuscript, and Bradley J. Sinclair, Bonn, for linguistic and substantial improvement of the text.

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Bonner zoologische Beiträge	Band 54 (2005)	Heft 4	Seiten 271–286	Bonn, Oktober 2006

The Genus *Achaenops* Suffrian, 1857 (Chrysomelidae: Cryptocephalinae), Designation of Neotypes and Description of New Species[1]

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Abstract. Described in 1857 by Eduard SUFFRIAN, the identity of the monotypic genus *Achaenops* remained doubtful. The type specimens were never re-examined after the original description and later lost when the collection of the Natural History Museum in Hamburg was destroyed. In this study, a neotype is designated for the generic type species *A. dorsalis.* Two other species described later in *Achaenops* were not found to be congeneric with *A. dorsalis*, and were transferred: *Lophistomus mandibularis* (Jacoby, 1901: 240) comb. nov. and *Acolastus nigrolineatus* (Bryant, 1944: 336) comb. nov. Four species originally described in *Cryptocephalus* are transferred to *Achaenops*: *Achaenops ruficornis* (Suffrian, 1857: 75) comb. nov., *Achaenops obscurellus* (Suffrian, 1857: 76) comb. nov., *Achaenops sericinus* (Suffrian, 1857: 80) comb. nov., and *Achaenops gilvipes* (Suffrian, 1857) comb. nov. *Protinocephalus weiseanus* Reineck, 1913: 648 was found to be a junior synonym of *A. gilvipes*, and consequently *Achaenops* Suffrian, 1857 (= *Protinocephalus* Reineck, 1913 syn. nov.). A neotype is designated for *C. obscurellus*. Lectotypes are designated for *Cryptocephalus ruficornis* and *C. gilvipes*. Two species are described as new to science from South Africa, *Achaenops punctatellus* sp. nov. from the Cape Peninsula and *Achaenops monstrosus* sp. nov. from the Western Cape. Male and female genitalia are figured for the first time. A map showing the collection sites is given.

Key words. Coleoptera, Achaenopina, South Africa, taxonomy

1. INTRODUCTION

The genus *Achaenops* was described by monotypy by SUFFRIAN (1857), who gave a detailed diagnosis for it. CLAVAREAU (1913) erected the tribe Achaenopini for this genus and no more genera were added to this tribe that is currently ranked as a subtribe Achaenopina of Cryptocephalini. There is no published record of a re-examination of the generic type species *A. dorsalis* after its original description. Consequently, the study of *A. dorsalis* is of interest for the understanding of the systematics of the Cryptocephalini. More specifically, it is the only subtribe of Cryptocephalini endemic to the Afrotropical Region. The designation of a neotype for *A. dorsalis* is necessary. Two species that were later described in *Achaenops* (JACOBY 1901; BRYANT 1944) are examined as well as types of Afrotropical species of *Cryptocephalus* and undetermined specimens in order to evaluate the diversity and distribution of *Achaenops*.

2. MATERIAL AND METHODS

The dried adults were dissected by separating the abdomen in water, the contents were soaked in cold diluted KOH and then washed in water. The eye length was measured in lateral view, the interocular space in frontal view.

Included in this study are specimens located in the following nine collections. The letter codens used in the text are according to the list "Abbreviations for Insect and Spider Collections of the World" (EVENHUIS & SAMUELSON 2005).

BMNH	Natural History Museum, London, Great Britain (J. Beard and S. Shute)
MESC	Matthias Schöller personal Collection, Berlin, Germany
MLUH	Martin-Luther-Universität Halle/Saale, Germany, Wissenschaftsbereich Zoologie (K. Schneider)
NHMB	Naturhistorisches Museum Basel, Switzerland (E. Sprecher and D. Burckhardt)
NMW	Naturhistorisches Museum Wien, Austria (H. Schönmann und H. Schillhammer)
SAMC	Iziko Museums of Capetown (South African Museum) Cape Town, South Africa (M. Cochrane)
SANC	South African National Collection of Insects, Pretoria, South Africa (E. Grobbelaar)
TMSA	South Africa, Gauteng, Pretoria, Transvaal Museum (R. Müller)
ZMHB	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (J. Frisch and M. Uhlig)

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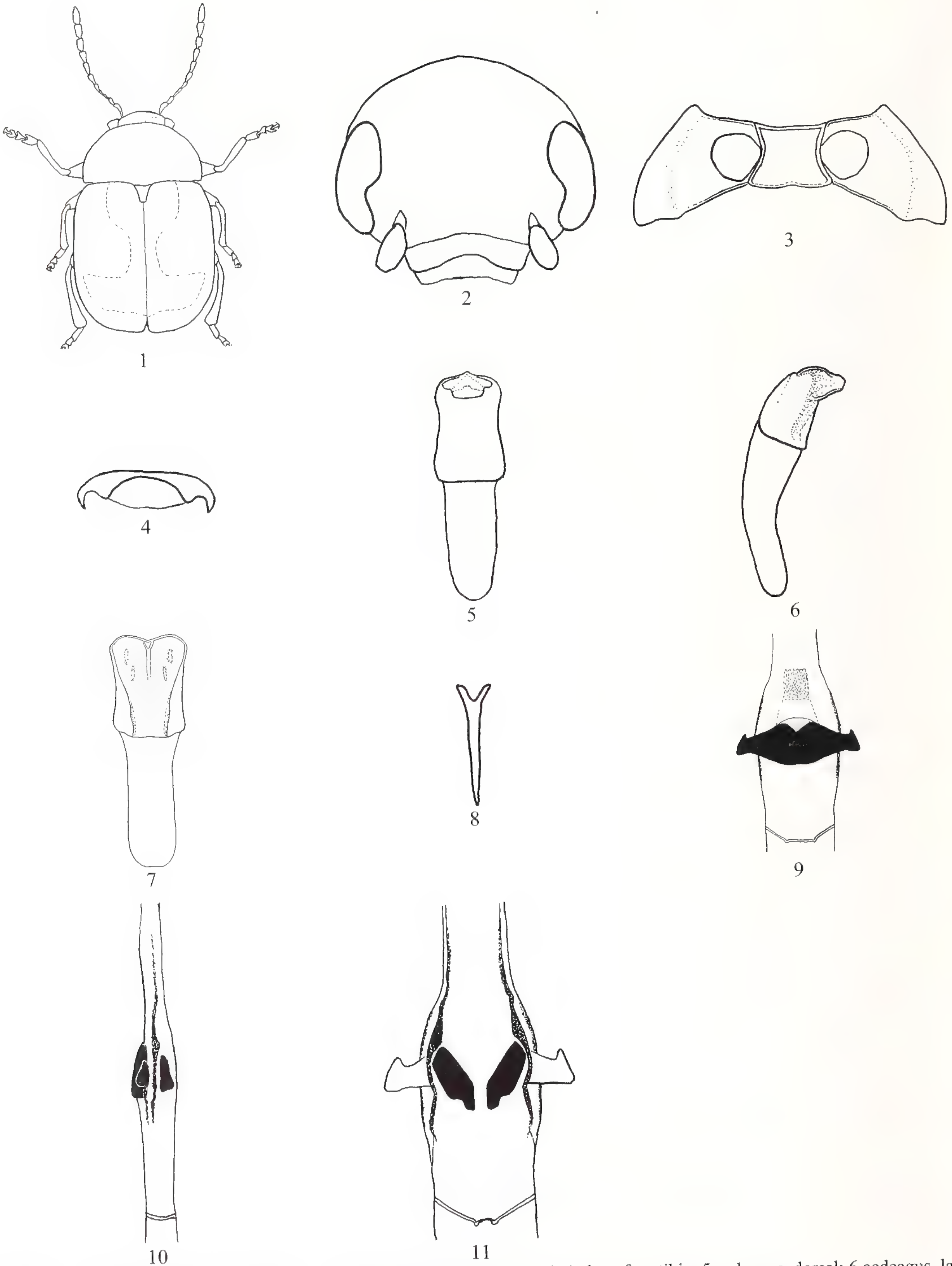
[1] Paper presented to the 6th International Symposium on the Chrysomelidae, Bonn, Germany, May 7, 2004.



Figs. 1-11. *Achaenops dorsalis*. 1 habitus; 2 head, frontal; 3 thorax ventral; 4 claw, fore tibia; 5 aedeagus, dorsal; 6 aedeagus, lateral; 7 aedeagus, ventral; 8 tergalapodem; 9 kotpresse, dorsal; 10 kotpresse, lateral; 11 kotpresse, ventral.

3. RESULTS

Achaenops dorsalis Suffrian, 1857 (Figs. 1-13)

Achaenops dorsalis Suffrian, 1857 (SUFFRIAN 1857: 236)

Type specimen. Neotype (male, NHMB): / Graaff-Reinet-Karroo Nat. Res., 830-1300 m, 24.X.1988 [white] / S. Afr., Cape Prov., W. Wittmer [white] / Neotypus *Achaenops dorsalis* SUFFRIAN, des. Matthias Schöller [red, printed] /.

A neotype is designated here in order to ensure the name's proper and consistent application.

Other specimens studied: 1f (MESC): South Africa, East Cape, Tsitsikamma nat. park, Storm river mouth, 34°01'S, 23°52'E, 5-11-1999, R. Constantin; 1m (BMNH): Mossel Bay, Cape Province, October 1921, R. E. Turner, Brit. Mus., 1921-450; 2m (BMNH): Mossel Bay, 1.-14.xi.1921, R. E. Turner, Brit. Mus., 1921-476; 1m (BMNH): Mossel Bay, 18.-30.xi.1921, R.E. Turner, Brit. Mus., 1922-2; 1m 1f (MESC) 2f (NHMB): Cape Province, Graaff-Reinet-Karroo Nature Reserve, 830-1300 m, 24.X.1988, leg. W. Wittmer; 1m (NHMB): Cape Province, Heidelberg, 12-24 km W, 05.XI.1988, leg. W. Wittmer & M.J.D. Brendell.

Type locality. The type locality of the neotype is approximately 32°41'S, 24°29'E, the collection locality of the lost types of Suffrian was Kaffernland, which means the territory of the Xhosa people in South Africa.

Diagnosis. A small orange-brown species with punctation of pronotum dense and coarse.

SUFFRIAN (1857) listed the short, ovate body and the distant eyes with shallow canthus as characters to differentiate *A. dorsalis* from species of *Cryptocephalus*.

Description of neotype (male)

Habitus. Body small, shape oval (Fig. 1), surface glabrous, size [mm]: length 1.8, width of elytra at humeri 1.0, length of pronotum 0.5, width 1.0.

Head. Head orange, regularly vaulted, glabrous, shiny, punctation sparse and coarse, head sunk into prothorax but still visible in dorsal view; clypeus punctate; eyes evenly convex, both laterally and longitudinally, eyes small, canthus shallow, triangular, eyes distant (Fig. 2), ratio of distance between upper lobes to eye length is 2.7 : 1.8., eye length about 2.5 x gena, gena with a rim for the first antennomere; antenna (Fig. 1) orange, antennomeres without circular sensillate depressions, antennomere 1 swollen, antennomeres 5-11 apically dilated, brown, longer than wide, clypeal area not distinctly separated, labial palpi acute.

Thorax. Pronotum: orange, punctation dense and coarse, interstices glabrous, shiny, all margins even, i.e., basal margin of pronotum without a row of teeth, lateral margins with a fine, narrow carina, only basal parts in posterior angles simultaneously visible in dorsal view; median lobe of basal margin truncate at apex but not raised; prosternal cavities closed; prosternal process transverse; ratio minimum width : length of prosternal process like 2:1.4, sides concave, apically and laterally with a fine ridge, apex concave (Fig. 3); scutellum triangular, elongate, glabrous, impunctate, without basal ridge, apically raised above elytra; elytra striate, scutellar row + 9 rows + marginal row, interstices glabrous; elytra apically rounded, reaching upper third of pygidium; epipleura long and broad, 4/5 the length of the elytra, with few punctures only, basal margin very fine; legs orange except for black claws; external edge of front tibiae not distinctly grooved; tarsi stout, first tarsomere of mid- and hind tarsi shorter than the following together; claws slightly dentate (Fig. 4).

Abdomen. Pygidium fuscous, side margins orange, sparsely and coarsely punctured, with short white setae, pygidium not visible in dorsal view; sternite 3 as long as sternites 4-7 along midline; lateral lobe at base of abdomen truncate; sternites orange with margins fuscous, densely and coarsely punctured, dull, with short white setae. Length of aedeagus 0.65 mm, apex with a fine tip (Fig. 5), bent in lateral view (Fig. 6) ventral side excavated with a central longitudinal ridge and four nodes (Fig. 7). Tergalapodem small, Y-shaped with apical branches very short (Fig. 8).

Description of female:

Habitus. Size [mm]: length 2.3, width of elytra at humeri 1.3, length of pronotum 0.6, width 1.1.

Head. Ratio of distance between upper lobes to eye length is 3.0 : 1.9.

Thorax. Pronotum: centre of basal margin black; Elytra: additional punctures between scutellar row and suture.

Abdomen. Pygidium orange, base fuscous, sparsely and coarsely punctured, pit of female abdomen very shallow, almost as long as wide, diameter shorter than length of sternite, base of pit weakly limited and covered with long setae; kotpresse (Figs. 9-11): dorsal sclerites large, length about 2 X width (Fig. 11), not attached to the broad sclerotization of the lateral fold (Fig. 10); posterior of the ventral band two weakly sclerotized areas are present which are not sharply delimited, one close to the middle of posterior margin of ventral band and the other, rectangular one not attached to the ventral band (Fig. 9).

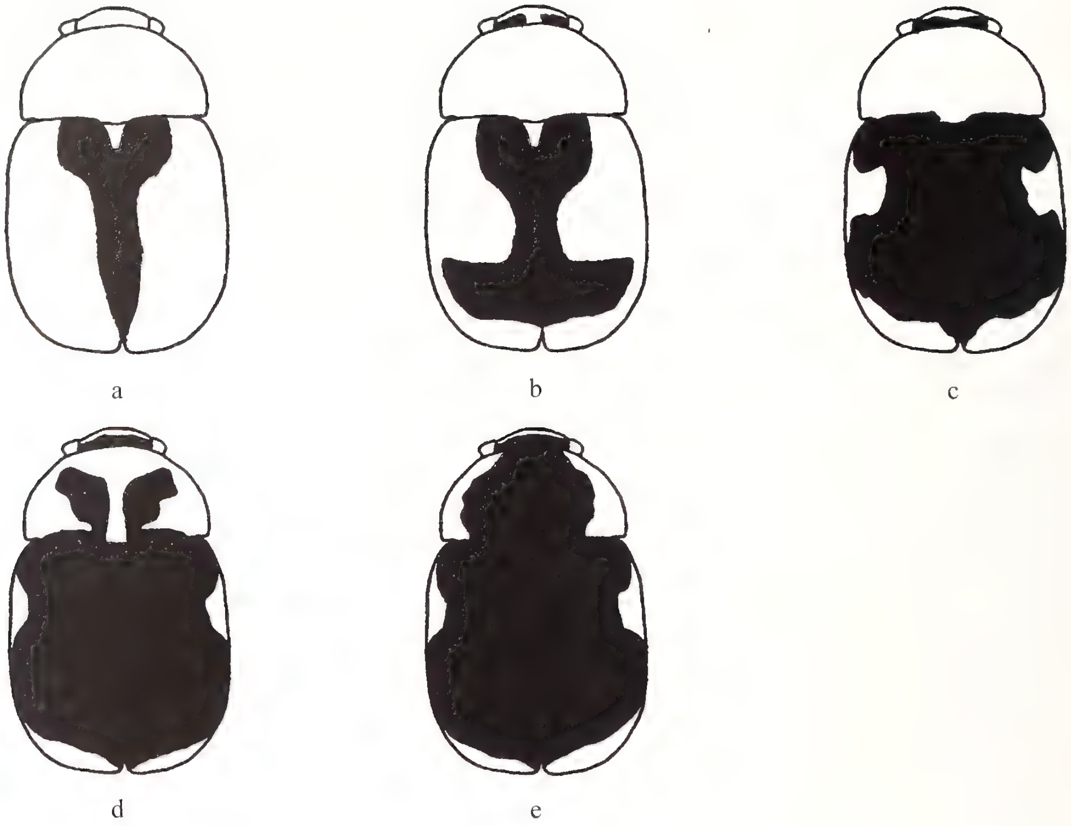


Fig. 12. Chromatic variability of *Achaenops dorsalis*.

Variability. The chromatic variability is shown in Fig. 12 a-e.

Distribution and biology. Known from four localities at the eastern part of the Western Cape and the western part of the Eastern Cape (Fig. 13). Figure 14 shows the habitat in Tsitsikama National Park (2xm).

Note. The neotype of *A. dorsalis* is in accordance with the original description by SUFFRIAN (1857). The description of *A. dorsalis* was based on a series of specimens located in the collection of the Natural History Museum Hamburg, Germany. The types in Hamburg were not found and are presumed to have been destroyed during World War II together with almost the complete collection of the museum in 1945. Moreover, the collections in Halle/Saale, Berlin (Germany) and Stockholm (Sweden), which harbour type specimens of SUFFRIAN were consulted, but unfortunately none of them had specimens of *A. dorsalis*.

Achaenops ruficornis (Suffrian, 1857) comb. nov. (Figs. 13, 15-16)

Cryptocephalus ruficornis Suffrian, 1857 (SUFFRIAN 1857: 75)

Type specimen. Lectotype *Cryptocephalus ruficornis* (female, ZMHB): / 23639 [white] / Pt. Natal Boh. [blue] / ruficornis (Boh*) Suffr.* [blue] / Type [red] / *Cryptocephalus ruficornis* Suffrian, 1857 Lectotypus designiert Matthias Schöller [red]/ *Achaenops ruficornis* (Suffrian, 1857), det. M. Schöller 2005 [white]/.

A lectotype was designated here in order to ensure the name's proper and consistent application.

Type locality. South Africa, Port Natal (Durban, 29°49'S 30°56'E).

Size. Length female lectotype 2.60, width of elytra at humeri 1.45, length of pronotum 0.90 and width 1.4.

Head. Eyes relatively large, ratio of minimum distance between upper lobes to eye length is 3.0 : 2.4.

Thorax. Claws relatively large, simple.

Female. Kotpresse with two small dorsal sclerites separated from the broad sclerotizations of the lateral fold (Fig. 15) and a ventral band (Fig. 16) terminating in two small apodemes.

Distribution and biology. Known only from the type locality.

Note. SUFFRIAN (1857: 75-76) gave a detailed description of this species. He mentioned male and female specimens communicated by Bohemann in ZMHB and Stockholm. I was only able to trace one female in

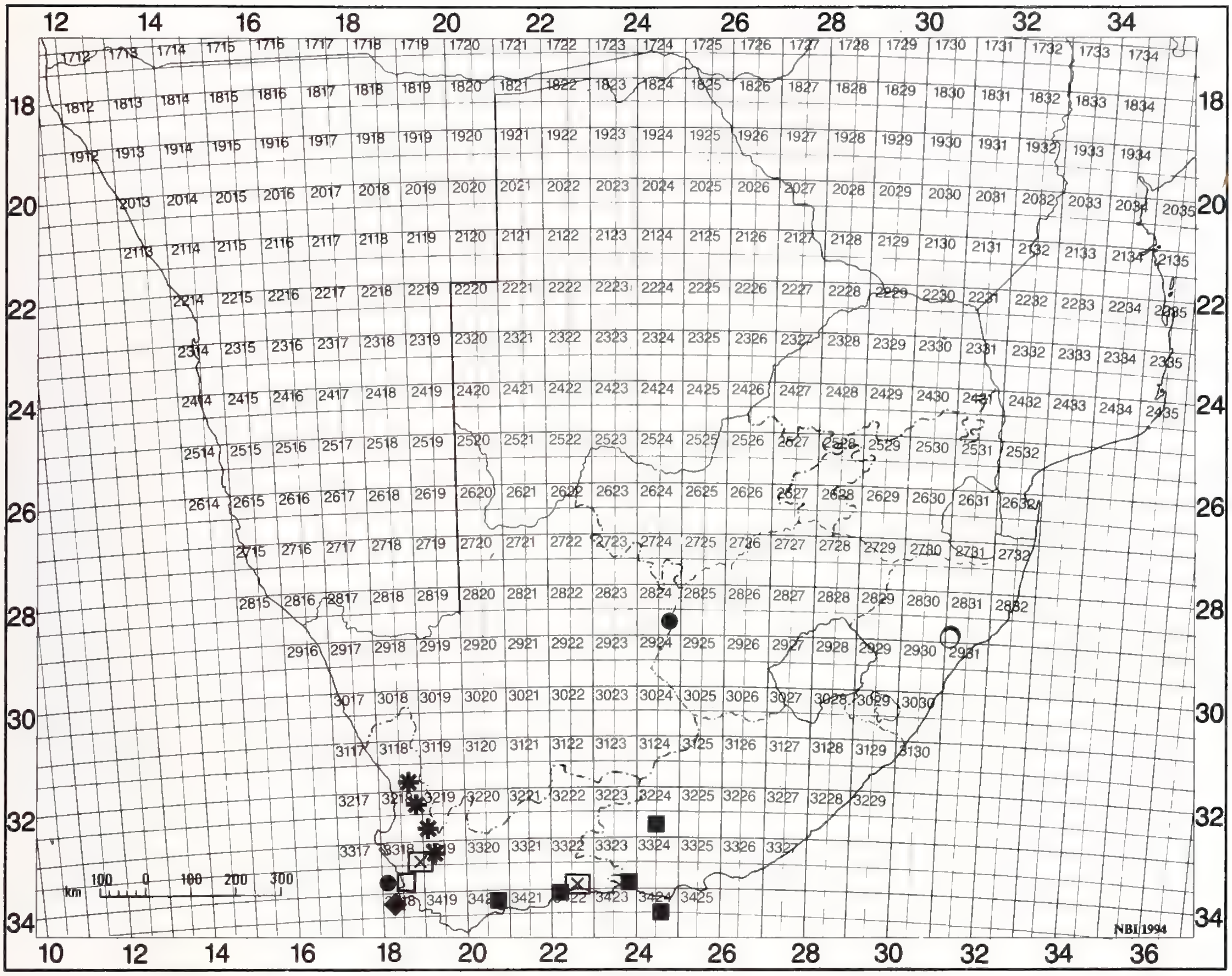


Fig. 13. Collection localities of *Achaenops* Suffrian; ■ = *A. dorsalis*, ○ = *A. ruficornis* (Natal), ◆ = *A. obscurellus*, ● = *A. sericinus*, □ = *A. punctatellus*, ⊠= *A. gilvipes*, ✱ = *A. monstrosus*.

ZMHB. *Achaenops ruficornis* is the first species SUFFRIAN (1857: 75) listed in his second species-group (2. Rotte) of *Cryptocephalus*, which comprised five species from South Africa.

Achaenops obscurellus **(Suffrian, 1857) comb. nov.** (Figs. 13, 17-27)

Cryptocephalus obscurellus Suffrian, 1857 (SUFFRIAN 1857: 76)

Type specimen. Neotype (male, SAMC): / South Africa, W. Cape pr. Cape Town, 34°13S 18°28E, Simon's Town, Miller Pt, 31.10.1999, R. Constantin [white label]/ Neotypus *Cryptocephalus obscurellus* des. Matthias Schöller [red, printed] / *Achaenops obscurellus* (SUFFRIAN, 1857), det. Matthias Schöller 2005 [white, printed] /.

A neotype is designated here in order to ensure the name's proper and consistent application.

Other specimens studied: 1m (MESC): South Africa, W. Cape pr. Cape Town, 34°13S 18°28E, Simon's Town, Miller Pt, 31.10.1999, R. Constantin; 1m (ZMHB), 1f (SANC), 1f (MESC): S. Africa, Western Cape, Cape Peninsula, Hout Bay, slope 500m S., 34°03'S, 18°21'E, 20 m, 18.10.2003, R. Constantin.

Type locality. The type locality of the neotype is Simon's Town, Miller Point (34°13'S 18°28'E), the collection locality of the lost types of SUFFRIAN was Kaffernland, which means the territory of the Xhosa people in South Africa.

Diagnosis. A small black species with shining, impunctate pronotum and pronotal and elytral side margins simultaneously visible in dorsal view, elytra with regular rows of punctures, and brown legs, differs from *A. dorsalis* and *A. punctatellus* in the structure of the pronotum, the aedeagus and the colouration.

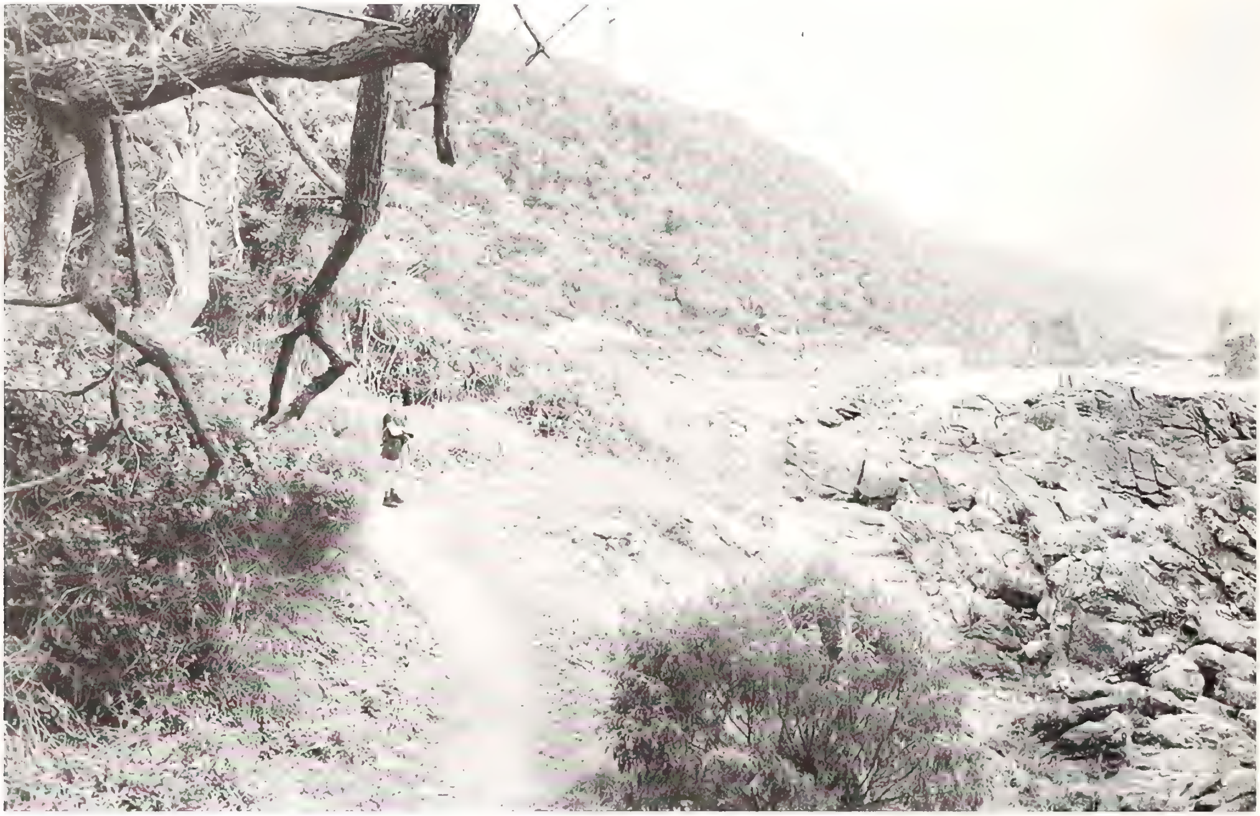
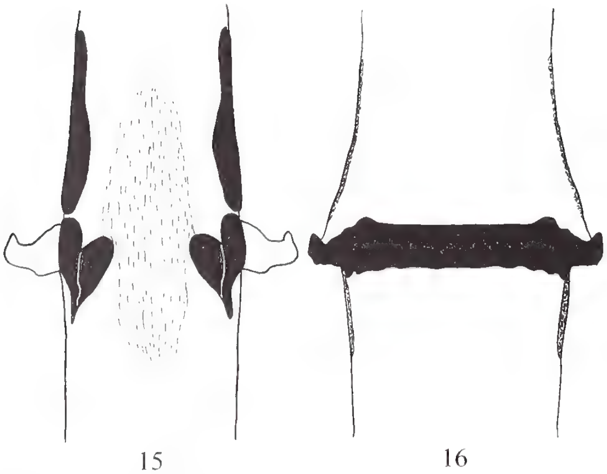


Fig. 14. Habitat of *Achaenops dorsalis*, Tsitsikamma National Park, South Africa. The "Mouth trail" along the seaside dominated by *Erica fourcadei, Erica* spp., many Asteraceae shrubs (*Chrysanthemoides monilifera*) on the border of a relict indigenous rain forest of *Podocarpus falcatus* and *P. latifolius*.



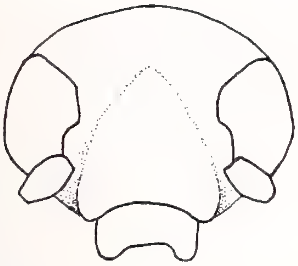
Figs. 15-16. *Achaenops ruficornis*. 15 kotpresse, dorsal; 16 kotpresse, ventral.

Description of neotype (male)

Habitus. Body small, shape oval; size [mm]: length 1.90, width of elytra at humeri 1.00, length of pronotum 0.50, width 1.00.

Head. Head visible in dorsal view, shiny, with coarse punctures; clypeus simple; labrum brown, mandibles brown, symmetric; eyes large and upper lobes approached (Fig. 17), ratio of minimum distance between upper lobes to eye length is 1.9 : 2.0; eye length about 4 X gena; canthus shallow and sinuate; antenna light brown, segments 6-11 black and apically expanded, antennae inserted low on frons; labial palpi acute.

Thorax. Pronotum shining and impunctate, with distinct margins, lateral margins with a fine, narrow carina and a row of punctures, simultaneously visible in dorsal view, median lobe of basal margin convex (Fig. 18); prosternal cavities closed, prosternal process transverse; scutellum elongate triangular (Fig. 19), without basal ridge, not apically raised above elytra, base without emargination; elytra with nine regular rows of punctures plus scutellar row which is not reaching the middle of the elytra plus marginal row, rows vanishing towards the base, interstices glabrous, lateral margins entirely simultaneously visible in dorsal view, elytra apically rounded, epipleuron half the length of the elytra, impunctate; legs brown, no tibial spurs, claws simple, small, apical margin of tarsomere 2 wider than tarsomere 1, fore tibia straight.



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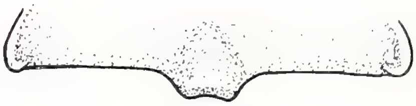

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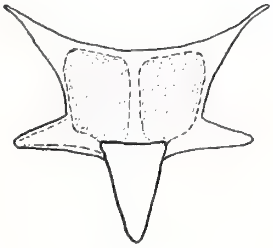

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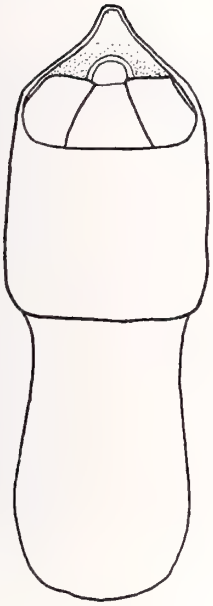

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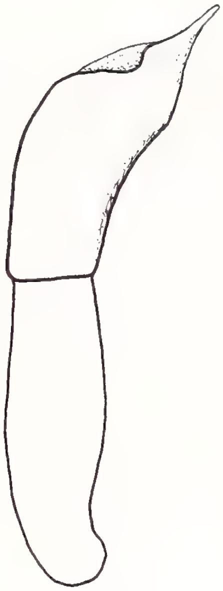

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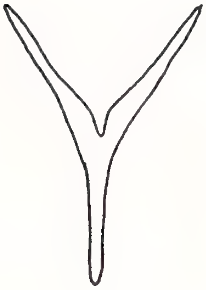

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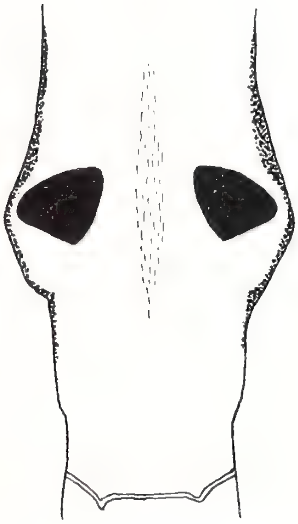

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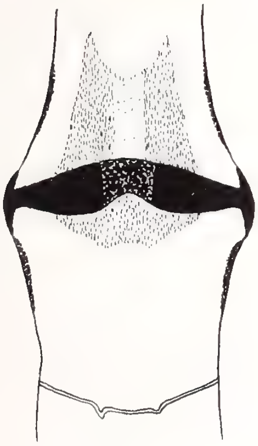

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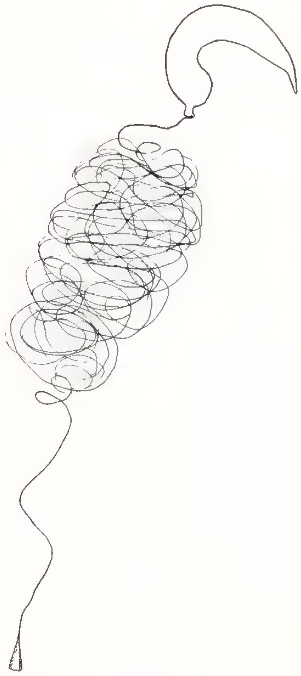

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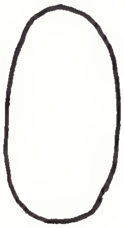

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Figs. 17-26. *Achaenops obscurellus*. 17 head, frontal; 18 basal margin of pronotum; 19 scutellum; 20 aedeagus, dorsal; 21 aedeagus, lateral; 22 tergalapodem; 23 kotpresse, dorsal; 24 kotpresse, ventral; 25 spermatheca; 26 egg.

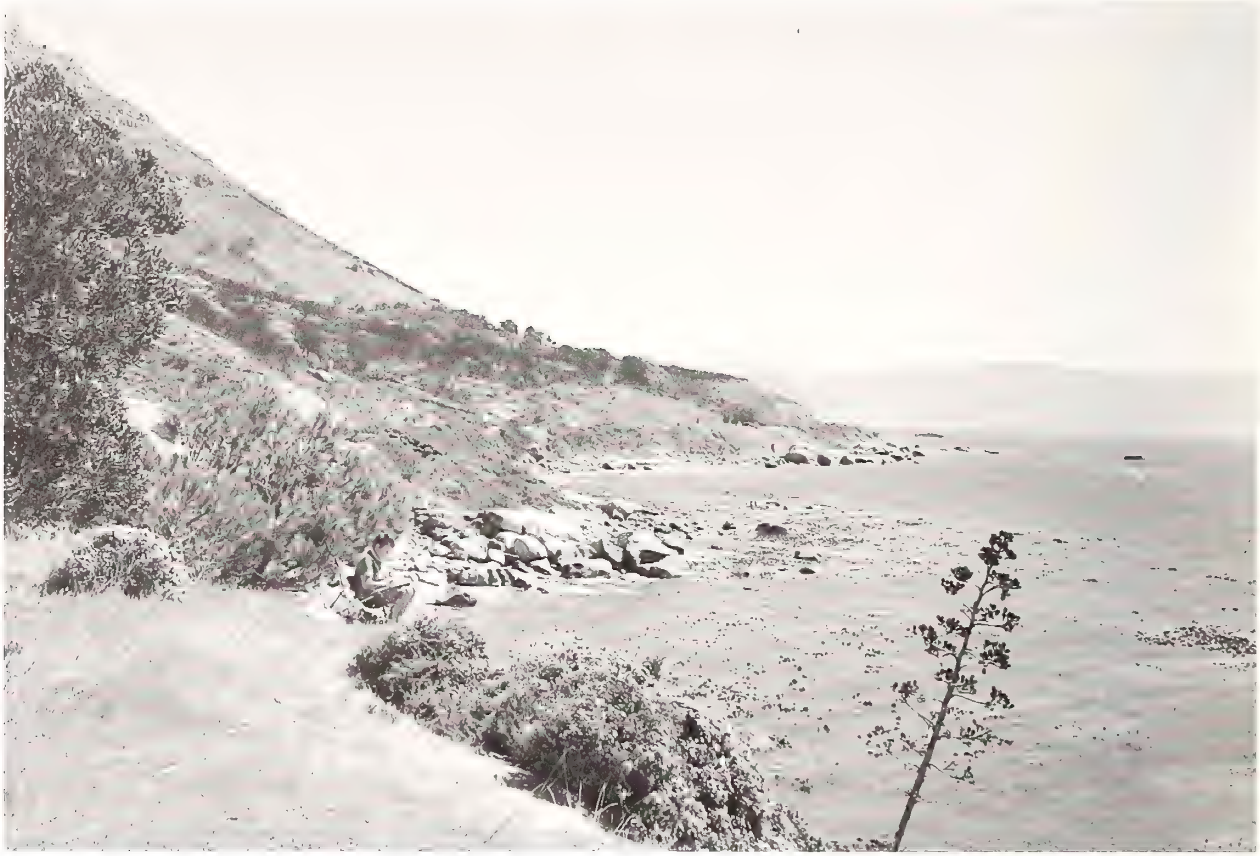


Fig. 27. Habitat of *Achaenops obscurellus*, Cape Peninsula, East coast South of Simon's Town at Miller's Point. A costal shrub dominated by *Erica* spp and *Felicia* spp. among some indigenous *Protea* and alien *Pinus* tree, South Africa.

Abdomen. Venter dark brown, sternites and pygidium with coarse punctures and short white setae, lateral lobe at base of abdomen rounded; elytra covering 50% of pygidium; aedeagus simple (Fig. 20), with ventral side regularly vaulted (Fig. 21), length of aedeagus 0.6 mm, tergalapodem Y-shaped (Fig. 22).

Description of female:

Habitus. Size [mm]: length 2.50, width of elytra at humeri 1.35, length of pronotum 0.65, width 1.25.

Head. As in male, but eyes more distant, ratio of minimum distance between upper lobes to eye length is 2.5 : 1.9.

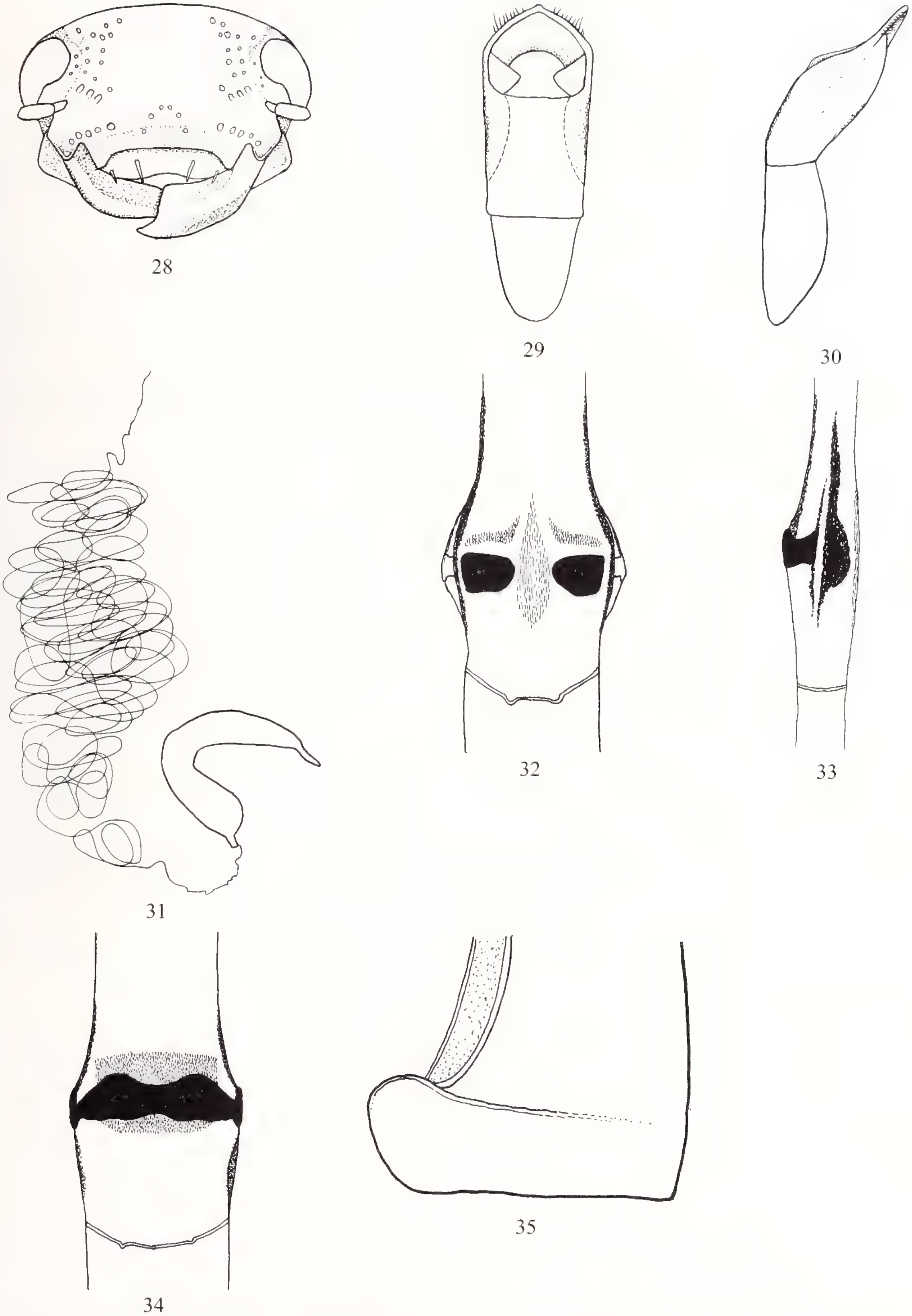
Abdomen. Kotpresse: dorsal sclerites triangular, not attached to the sclerotization of the lateral fold, dorsal fold slightly sclerotized (Fig. 23), posterior of the ventral band a trapeziform, sclerotized area, and another sclerotized area close to the middle of anterior margin of ventral band (Fig. 24); spermatheca (Fig. 25), spermathecal ductus coiled up and base extended; an egg found during dissection was longitudinal oval (Fig. 26).

Variability. No significant variability was detected.

Distribution and biology. Known from two localities on the Cape Peninsula (Fig. 13). Figure 27 shows the habitat on Miller Point.

Note. The neotype of *A. obscurellus* is in accordance with the original description by SUFFRIAN (1857). The description of *A. obscurellus* was based on a single female specimen located in the collection of the Natural History Museum Hamburg, Germany, but it is presumed destroyed (see above under *A. dorsalis*). Moreover, the collections in Halle/Saale, Berlin (Germany) and Stockholm (Sweden), which harbour type specimens of SUFFRIAN were consulted, but none of them had a specimen of *A. obscurellus*.

Achaenops obscurellus is the second species SUFFRIAN (1857: 75) listed in his second species-group (2. Rotte) of *Cryptocephalus,* which comprised five species from South Africa.



Figs. 28-35. *Achaenops gilvipes*. 28 head, frontal; 29 aedeagus, dorsal; 30 aedeagus, lateral; 31 spermatheca; 32 kotpresse, dorsal; 33 kotpresse, lateral; 34 kotpresse ventral; 35 lateral lobe at base of abdomen.

***Achaenops gilvipes* (Suffrian, 1857) comb. nov.** (Figs. 13, 28-35)

Cryptocephalus gilvipes Suffrian, 1857 (SUFFRIAN 1857: 77)

Protinocephalus weiseanus Reineck, 1913 (REINECK 1913: 648) syn. nov.

Type specimens. Lectotype *Cryptocephalus gilvipes* (male, MLUH): /29252 (red ink) [white]/ MLU Halle, WB Zoologie, S.-Nr. 7/1/5 [white]/ *Cryptocephalus gilvipes* Suffrian, 1857 Lectotypus designiert Matthias Schöller [red]/ *Achaenops gilvipes* (Suffrian, 1857), det. M. Schöller 2005 [white]/.

A lectotype was designated here in order to ensure the name's proper and consistent application.

In his notebook preserved in Halle, Germany, SUFFRIAN wrote for the specimen no. 29252: "von Thorey erhalten (received from Thorey)", Thorey was also mentioned in the original description.

3 Paralectotypes (females, MLUH): /22791 (red ink) [white]/ MLU Halle, WB Zoologie, S.-Nr. 7/1/5 [white]/; 23711 (red ink) [white]/ MLU Halle, WB Zoologie, S.-Nr. 7/1/5 [white]/; 29251 (red ink) [white]/ MLU Halle, WB Zoologie, S.-Nr. 7/1/5 [white]/; all three with my labels: *Cryptocephalus gilvipes* Suffrian, 1857 Paralectotypus designiert Matthias Schöller [red]/ *Achaenops gilvipes* (Suffrian, 1857), det. M. Schöller 2005 [white]/.

Holotype *Protinocephalus weiseanus* (male, MLUH): /Caffrar, Thorey (ink) [blue]/ *gilvipes* Suffr. Typ (ink) [blue]/ ex coll. J. Weise [white]/ Type [red]/ *Protinocephalus Weiseanus* Rk. (ink) [white]/ (my label) Holotypus *Protinocephalus weiseanus* REINECK vid. Schöller XI 1996 [red]/ *Achaenops gilvipes* (Suffrian, 1857), det. M. Schöller 2005 [white]/.

Other specimens studied: 1 female, NHMW: Cape, 1867. Note: this record was published in Reineck, 1915 (as *Cryptocephalus gilvipes*); 2 females BMNH: E. Coll. Chevt., 6756, 273 and 6756, 275; 1 male BMNH, Cape Province, George, 15.-17.XI.1921.

Characters not mentioned in previous descriptions.

Head. Male with enlarged mandibles (Fig. 28) and gena with triangular projections.

Abdomen. Apex of aedeagus (Fig. 29) slightly bend upwards, with a small apical tip, ventral side regularly vaulted (Fig. 30). Length of aedeagus 0.6 mm.

Female. Spermatheca (Fig. 31) hook-shaped, slender, spermathecal ductus long and thin, densely coiled up; kotpresse: dorsal sclerites large, two slender sclerotized areas posterior to the dorsal sclerites, dorsal fold slightly sclerotized (Fig. 32), lateral fold strongly sclerotized (Fig. 33), posterior of the ventral band a rectangular sclerotized area, and another sclerotized area close to the middle of anterior margin of ventral band (Fig. 34); lateral lobe at base of abdomen rounded (Fig. 35).

Variability. No significant variability was detected.

Distribution. All specimens except for one male from the Western Cape (Fig. 13) were collected in the 19th century without exact data.

Note. *Achaenops gilvipes* is the third species SUFFRIAN (1857: 75) listed in his second species-group (2. Rotte) of *Cryptocephalus,* which comprised five species from South Africa.

***Achaenops sericinus* (Suffrian, 1857) comb. nov.** (Figs. 36-40)

Cryptocephalus sericinus Suffrian, 1857 (SUFFRIAN 1857: 80)

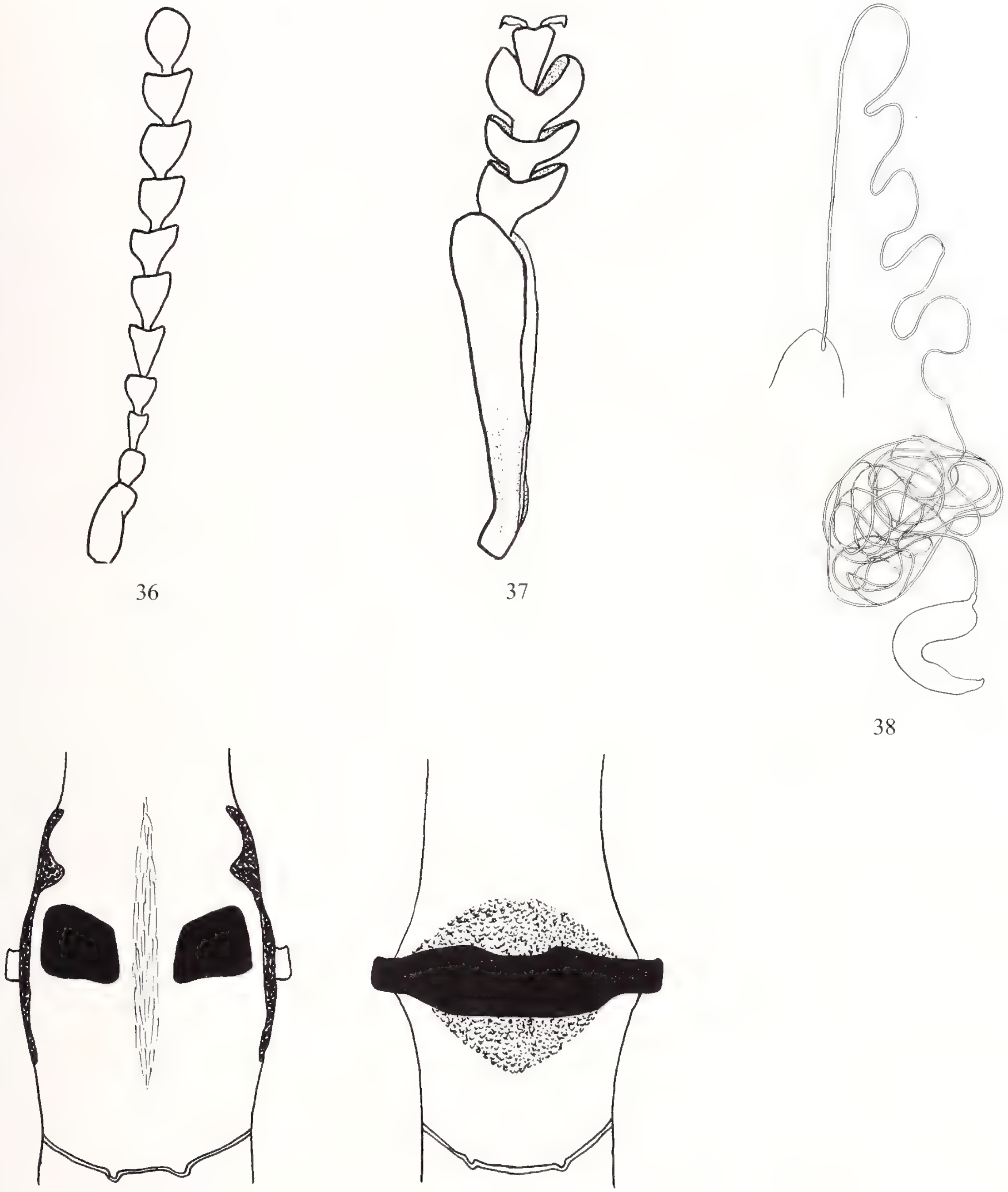
Type specimen. Holotype (female, MLUH): 21756 [white label, red ink]/ HOLOTYPUS *Cryptocephalus sericinus* Suffrian, 1857; vid. Matthias Schöller [red, printed] / *Achaenops sericinus* (Suffrian, 1857) det. Matthias Schöller 2003.

Other specimens studied: 1f (SAMC) / Kimberley Bro. Power 1912 [white] / South African Museum Cape Town (SAMC) [white] /; 1f (SAMC) / CT 10.86 [white] / South African Museum Cape Town (SAMC) [white] /.

Size [mm]: length 3.1-3.4, width of elytra at humeri 1.6-1.7, length of pronotum 0.95-1.05, width 1.6

Head. Head shagreened and punctation dense, head sunk into prothorax; eyes evenly convex, both laterally and longitudinally, eyes relatively small, distant, ratio eye width : length 1.4 : 2.4, ratio of distance between upper lobes to eye length is 1.9 : 1.2, canthus shallow; antennal segments 1-5 yellowish orange, 6-11 brown and apically expanded, antenna (Fig. 36) 0.36 x body length.

Thorax. Pronotum: shagreened and punctation dense; lateral margins even, simultaneously visible in dorsal view; median lobe of basal margin truncate, slightly raised; prosternal process narrow, ratio minimum width: length like 1:2.5, sides concave, apically with a fine ridge, apex concave; scutellum triangular, glabrous, shagreened and impunctate, without a basal ridge, not apically raised above elytra; elytra semistriate, center of rows 1-3 confused, and other rows might be disturbed by additional punctures, too; interstices shagreened, microstructures round, elytra apically rounded, reaching upper third of pygidium; epipleura long, ¾ the length of the elytra, with few small punctures only; external edge of tibiae distinctly grooved (Fig. 37); claws appendiculate.



Figs. 36-40. *Achaenops sericinus*. 36 right antenna; 37 right fore leg; 38 spermatheca; 39 kotpresse, dorsal; 40 kotpresse, ventral.

Abdomen. Pygidium densely punctured, shagreened, dull, female abdomen with deep longitudinal pit of equal diameter to length of sternite, base of pit straigth, sternite 3 as long as sternites 4-7 along midline; lateral lobe at base of abdomen rounded; sternites dark brown, chagreened, with sparse punctation and short white setae.

Spermatheca and kotpresse: spermathecal ductus long, simple (i.e. not spiral), coiled up voluminous ball-like close to the spermatheca, insertion to vaginal sac slightly inflated (Fig. 38). kotpresse: dorsal sclerites large, dorsal fold slightly sclerotized (Fig. 39), lateral fold strongly sclerotized, posterior to the dorsal sclerites a tooth-like extension, anterior and posterior of the ventral band a triangular sclerotized area (Fig. 40).

Variability. No significant variability was detected.

Distribution and biology. Indicated from two localities, Kimberley (28°43'S 24°44'E) in the eastern Northern Cape and Cape Town (33°55'S 18°26'E), but both records are not unambiguous collection localities and need confirmation.

Note. *Achaenops sericinus* is the fifth species SUFFRIAN (1857: 75) listed in his second species-group (2. Rotte) of *Cryptocephalus*, which comprised five species from South Africa.

Achaenops punctatellus sp. nov. (Figs. 41-45)

Type specimens. Holotype (female, MLUH): 19196 [white label, red ink]/ Holotypus *Achaenops punctatellus* MIHI, des. Matthias Schöller [red, printed] /.

Note: a new piece of cardboard was used to glue the specimen, and the original cardboard was kept on the original pin, too.

3 Paratypes: 1m (BMNH) / Table Mt. Cape of G. Hope, W. Bevins, 1906-167 [white, blue line]/; 1m (SAMC) / Cape Town J. Pureell 1886 (ink) / South African Museum Cape Town (SAMC) [white] /; 1f (BMNH) / Camps Bay, Cape Peninsula, 1-20.x.1920 [white] / S. Africa E. Turner 1920-423. [white, blue line]/; all paratypes with my label Paratypus *Achaenops punctatellus* MIHI, des. Matthias Schöller [red, printed] /.

Diagnosis

A brown species with tibia and femur yellowish orange and pronotum shagreened and punctured, differs from *A. dorsalis* in the structure of the pronotum and the colouration, and from *A. sericinus* in the colour of the legs and the envaginated clypeus.

Description of Holotype (female)

Size [mm]: length 2.40, width of elytra at humeri 1.30, length of pronotum 0.60 and width 1.20.

Head. Head visible in dorsal view, shagreened, with coarse punctures, labrum and mandibles yellow; labial palpi acute; eyes small and upper lobes distant, therefore ratio of distance between upper lobes to eye length is 2.25 : 1.00, eyes evenly convex, relatively small, canthus deep; segments 1-3 of antennae yellowish orange, 4-11 brown, 5-11 apically expanded, antennae inserted low on frons.

Thorax. Pronotum with distinct margins, basal margin of pronotum without a row of teeth, lateral margins even, not simultaneously visible in dorsal view; median lobe of basal margin truncate, slightly raised, expanded but not impressed prior to the expansion; punctures only on disk of pronotum, very shallow and moderately dense, interstices glabrous; prosternal cavities closed; scutellum triangular, not apically raised above elytra; elytra with punctation striate, 9 regular rows plus scutellar row which is not reaching the middle of the elytra, interstices glabrous; epipleuron half the length of the elytra; tibia and femur yellowish orange, external edge of tibiae simple, tarsi brown, claws simple, small; no tibial spurs.

Abdomen. Venter brown, sternites and pygidium with coarse punctures and short white setae, pygidium shagreened; kotpresse (Fig. 41): dorsal sclerite not attached to the sclerotization of the lateral fold, an extension directed towards the dorsal fold, posterior of the dorsal sclerite, a linear twig of the sclerotization of the lateral fold directed towards the dorsal fold; dorsal fold slightly sclerotized, posterior of the ventral band a diffuse, weakly sclerotized additional band is present, and another sclerotized area close to the middle of anterior margin of ventral band; spermatheca relatively small, spermathecal ductus coiled up densely close to the spermatheca (Fig. 42).

Description of male. Head: clypeus V-shaped envaginated, mandible asymmetric (Fig. 43); size [mm]: length 2.05, width of elytra at humeri 1.10, length of pronotum 0.6, width 1.05; length of aedeagus 0.55 mm, tip moderately acute, orificium large (Fig. 44), with four internal sclerites visible, ventral side regularly vaulted (Fig. 45).

Variability. In the female paratype, segments 1-4 of the antennae and the first two tarsal segments are yellow.

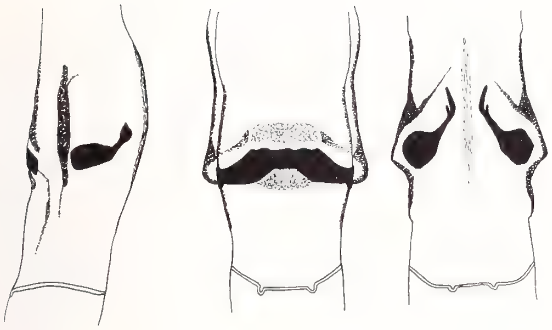
Etymology. The name *punctatellus* was proposed by SUFFRIAN in his notebook preserved in Halle, Germany. It is a Latin adjective.

Distribution and biology. Known from the surroundings of Cape Town only. No information on the biology is available.

Achaenops monstrosus sp. nov. (Figs. 46-53)

Type specimens. Holotype (male, SANC): / SOUTH AFRICA, C.P. Middelberg Pass nr Citrusdal, 32.38S 19.09E. 19.ix.1986 R. Oberprieler [white] / collected on *Protea nitida* [white] / NATIONAL COLL. OF INSECTS Pretoria, S. Afr. [white] / Holotypus *Achaenops monstrosus* MIHI, des. Matthias Schöller [red] /.

5 Paratypes: 1f (SANC) / SOUTH AFRICA, C.P. Middelberg Pass nr Citrusdal, 32.38S 19.09E. 19.ix.1986 R. Oberprieler [white] / collected on *Protea nitida* [white] /; / 1m, 1f (SANC) / SOUTH AFRICA, C.P. Gydo Pass near Prince Alfred, 33.14S 19.20E. 19.ix.1986 R. Oberprieler [white] / collected on *Protea nitida* [white] /; 1f (NHMB) / Süd Afrika Cape Prov. W. Wittmer [white] / Algeria Cederberg 520/1200m 10.X.1990 [white] /; / 1m (TMSA) / S.Afr. ;SW Cape Prov., Wiedow farm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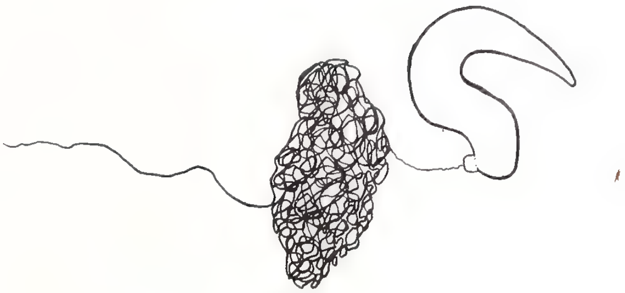
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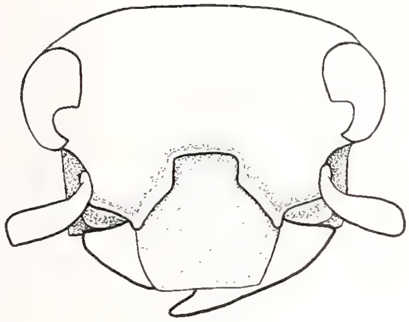
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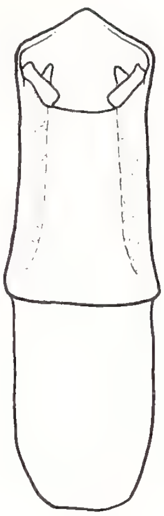
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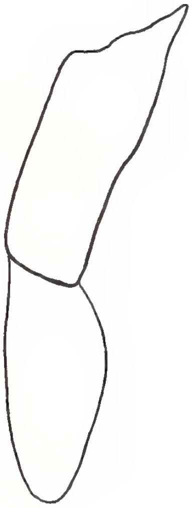
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Figs. 41-45. *Achaenops punctatellus*. 41 kotpresse (lateral, ventral, dorsal); 42 spermatheca; 43 head, frontal; 44 aedeagus, dorsal; 45 aedeagus, lateral.

31.46 S – 18.46 E [white] / 12.9.1987; E-Y: 2492 fynbos vegetation leg. Endrödy-Younga [white] /; all paratypes with my label Paratypus *Achaenops monstrosus* MIHI, des. Matthias Schöller [red, printed] /.

Diagnosis

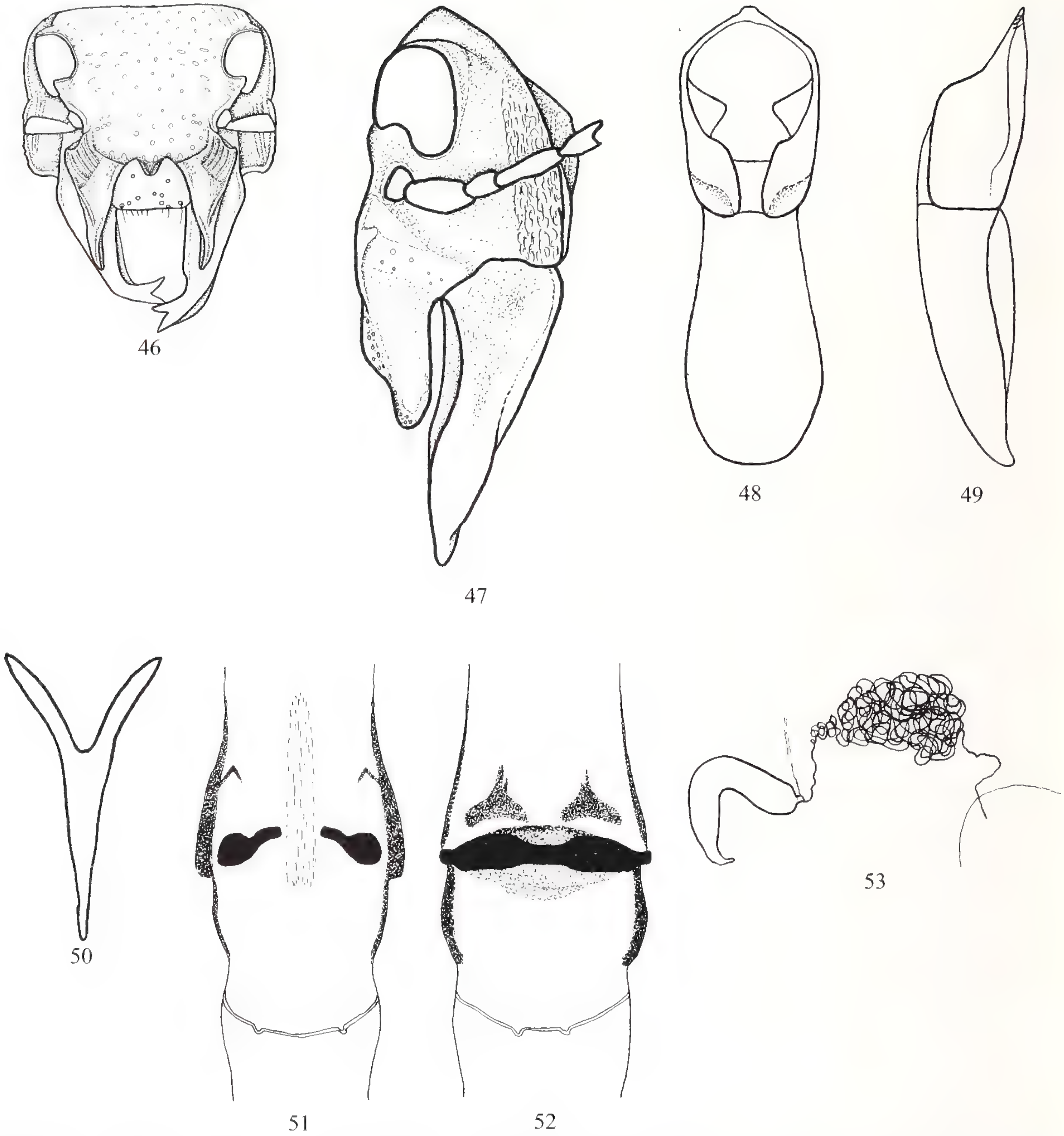
A large black species with tip of mandibles and base of antennae brown, male with extremely enlarged clypeus and mandibles and pronotum not shagreened.

Description of Holotype (male)

Habitus. Body large, shape cylindrical, size [mm]: length 3.50, width of elytra at humeri 1.80, length of pronotum 1.20, width 1.90.

Head. Head visible in dorsal view, shiny, punctation sparse and coarse, clypeus with two acute thorns and a median triangular extension (Fig. 46), labrum brown, mandibles large, black with reddish-brown apex, apex with three teeth, asymmetric with left mandible larger; eyes comparatively small and upper lobes distant, therefore ratio of minimum distance between upper lobes to eye length is 2.0 :1.0, eye length about 2 x gena (Fig. 47); canthus normal and sinuate; antenna black, first two segments brown, segments 4-11 apically expanded, antennae inserted at lower third of frons; labial palpi acute.

Thorax. Pronotum shiny and impunctate, but surface of pronotum irregularly undulated (seen at high magnification), with distinct margins, lateral margins with a fine, narrow carina and a row of punctures, simultaneously visible in dorsal view, median lobe of basal margin convex; prosternal process transverse; scutellum elongate triangular, without basal ridge, not apically raised above elytra, base without emargination; elytra with nine regular rows of punctures plus scutellar row which is not reaching the middle of the elytra plus marginal row, interstices glabrous, with very fine wrinkles, lateral margins not simultaneously visible in dorsal view, basal margin without carina, elytra raised around scutellum, elytra apically rounded, epipleuron 2/3 the length of the elytra, apically with a row of punctures; legs black, no



Figs. 46-53. *Achaenops monstrosus*; 46 head frontal; 47 head, lateral; 48 aedeagus, dorsal; 49 aedeagus, lateral; 50 tergalapodeme; 51 kotpresse, dorsal; 52 kotpresse, ventral; 53 spermatheca.

tibial spurs, fore tibiae bend, about 1/3 longer than mid and hind tibiae, apically extended, claws relatively small, dentate, apical margin of tarsomere 2 wider than tarsomere 1.

Abdomen. Venter black, sternites and pygidium with coarse punctures and short white setae; elytra covering 50% of pygidium; aedeagus with dorsal side weakly sclerotized along the median line (Fig. 48), with a rounded tip, almost straight in lateral view (Fig. 49), with ventral side regularly vaulted, length of aedeagus 0.9 mm; tergalapodeme simple, y-shaped (Fig. 50).

Description of female

Clypeus prominent, with shallow projections ventral to the antennae, but without thorn-like projections; eyes small and upper lobes distant, therefore ratio of minimum distance between upper lobes to eye length is 2.4 : 1.3; fore tibiae only slightly longer than hind tibiae, and only slightly bent; abdominal pit shallow, almost as long as wide, sides straight; kotpresse: dorsal sclerites slender, with an extension directed towards the dorsal fold (Fig. 51), posterior of the dorsal sclerite, a rectangular bent twig of the sclerotization of the lateral fold directed towards the dorsal fold, dorsal fold slightly sclerotized; posterior of the ventral band (Fig. 52), two sclerotized patches are present, and another two sclerotized areas attached to the anterior and posterior margins of the ventral band, respectively; spermatheca (Fig. 53), spermathecal ductus coiled up.

Variability. Size [mm] (mean (max., min., n)): length of male 3.27 (3.50, 3.00, 3.00), female 3.53 (3.60, 3.50, 3.00), width of elytra at humeri in male 1.73 (1.80, 1.70), female 1.77 (1.80, 1.70), length of pronotum in male 1.07 (1.20, 0.90), width 1.80 (1.90, 1.80) length in female 1.00 (1.00, 1.00) and width 1.92 (1.95, 1.90). The puncturation on the clypeus is more dense and coarse in the male from Wiedow farm.

Etymology. This species is named after the monstrous appearance of the male's head. It is a Latin adjective.

Distribution and biology. Known from the northern part of the Western Cape (Fig. 13); collected on wagon tree or waboon, *Protea nitida* Philip Miller, a shrub or tree up to 9 m which is growing typically on drier, lower slopes from 0-1200 m NN on gravely acid sandy soil.

Species to be transferred to other genera.

Two more species described in *Achaenops* (JACOBY, 1901; BRYANT, 1944) were found neither to be congeneric nor to belong to *Achaenops*. This illustrates the need for a neotype for *A. dorsalis* in the sense of article 75.3 of the International Code of Zoological Nomenclature. The two species have to be transferred to other genera:

***Lophistomus mandibularis* (Jacoby, 1901) comb. nov.**

Achaenops mandibularis Jacoby, 1901 (JACOBY 1901: 240)

***Acolastus nigrolineatus* (Bryant, 1944) comb. nov.**

Achaenops nigrolineatus Bryant, 1944 (BRYANT 1944: 336)

4. DISCUSSION

SUFFRIAN (1857) placed *Achaenops dorsalis* between *Cryptocephalus* and *Acolastus* because of its habitus, shape of the head and the movability of the pronotum, the latter was a character which was of special importance to SUFFRIAN for generic classification. *Achaenops dorsalis* has an oval habitus, whereas the species described in *Cryptocephalus* by SUFFRIAN and transferred to *Achaenops* in this study have a more or less cylindrical habitus. All species of SUFFRIAN's (1857) second species group (=2. Rotte) of *Cryptocephalus* were transferred to *Achaenops*, except for *C. atratulus*, the holotype of which was examined during this study and found to belong to *Cryptocephalus*. The short diagnosis of the second species group is in accordance with the diagnosis of *Achaenops* by SUFFRIAN, except for the cylindrical habitus. The female genitalia, studied here for the first time, are homogeneous. The spermatheca is hook-shaped, and the spermathecal ductus is coiled up densely. The arrangement of the sclerites of the kotpresse is homogeneous, too. The lateral fold is strongly sclerotized, and a pair of dorsal sclerites is present which are not attached to the lateral fold. Ventrally, a band-like sclerite is present. The species differ in the shape of the dorsal sclerites as well as in the presence or absence, or shape of sclerotized areas close to the ventral band. The male genitalia show few external characters, however, the shape differs well enough to separate species, especially in lateral view. The ventral side of the aedeagus is regularly vaulted in all species except for *A. dorsalis*.

The history of the genus *Protinocephalus* is curious; REINECK (1913) published the genus based on a single male specimen. In 1915, he published a large paper on Afrotropical Cryptocephalinae including females of *A. gilvipes*, but he did not recognise that the female specimens belonged to the male he described as *P. weiseanus*. *Protinocephalus* was published too late to be included in the catalogue of Cryptocephalinae (CLAVAREAU 1913) and was never re-examined. I found the holotype in a drawer with in-litteris specimens in ZMHB.

The only known plant *Achaenops* was collected from is *Protea*. Future studies will show if *Achaenops* is associated with the fynbos-vegetation.

In this publication, two new species were described to illustrate the variability of the genus. There are more undescribed species, a total of at least 25 species. A key to the species of *Achaenops* and a revised diagnosis for the genus will be given later together with the description of the remaining species.

Acknowledgements. I would like to thank Dr. Robert Constantin, Saint-Lo, France, for the communication of specimens and habitat pictures, and the colleagues listed in Materials and Methods for the allowing the loan of specimens from the respective museum collections. Dr. Horst Kippenberg, Herzogenaurach, Germany and an anonymous reviewer made valuable suggestions to improve the manuscript.

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Bonner zoologische Beiträge	Band 54 (2005)	Heft 4	Seiten 287–295	Bonn, Oktober 2006

Failure-time Analyses of the Effectiveness of Larval Shield Defenses in Tortoise Beetles (Chrysomelidae: Cassidinae)[1]

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Abstract. Plant chemistry and predation are thought to be major factors responsible for the recurrent evolution of dietary specialization in herbivorous insects. However, their relative importance and the degree to which they interact to drive diet evolution remain unknown. The present study aims to test predictions of the 'nasty host plant hypothesis', which posits that an herbivore's diet becomes more restricted as its reliance upon novel host plant compounds that confer protection from predators increases. The tortoise beetle larval shield system affords a unique opportunity to examine how predation and host plant chemistry interact. Shields can be micro-manipulated, including removal, chemical modification and reattachment, without harm to the larvae. We subjected larvae of different diet breadths produced from basal and derived hosts to a predation bioassay and compared the relative effectiveness of their shields under different treatment conditions. Failure-time analyses, the most appropriate statistical approach for right-censored temporal data, revealed that specialist larvae were consistently less susceptible to predation than were generalists feeding on the same plant. Although generalists were as competent as specialists at handling non-polar host chemistry, specialists were better at manipulating more polar host-derived compounds, which are more likely to include novel chemistry. Host shifts may be constrained to only those plants that possess novel, polar compounds. The interaction between plant chemistry and beetle diet evolution may be one of escalation driven by predation, wherein specialists are increasingly more effective than generalists in the assimilation of host plant polar compounds into shield defenses.

Key words. Chrysomelidae, larval shield, *Azteca*, tortoise beetle, Hispinae, predation, chemical defense, failure-time analysis

1. INTRODUCTION

Approximately three-quarters of Earth's biodiversity is involved in a tri-trophic interaction among plants, herbivorous insects, and insect enemies (STRONG et al. 1984; SOUTHWOOD 1996). However, herbivory represents an ecological obstacle that few groups have been able to surmount and only nine of twenty-nine insect orders have succeeded in colonizing the plant resource spectrum. The vast majority of herbivorous insects are members of either the Lepidoptera or the Coleoptera. Chief among the many obstacles to plant-feeding are (1) bottom-up, plant related physiological factors, and, (2) top-down, ecological factors (FUTUYMA & KEESE 1992; DYER & FLOYD 1993). The major bottom-up obstacle is plant secondary chemistry, i.e., those compounds not involved in photosynthesis or respiration. Over 20 thousand such compounds have been discovered so far and most of them have known resistance or defensive functions. The major top-down obstacle is predation.

What is the relationship between the astonishing array of plant secondary compounds and insect enemies? The fact is that the vast majority of herbivorous insects are dietary specialists that can feed on only one or a few related plants (EHRLICH & RAVEN 1964; FUTUYMA & KEESE 1992; BERNAYS & CHAPMAN 1994). Why an insect would evolve a narrower, rather than a broader diet, presents an ecological conundrum: the likelihood of failing to locate a suitable host plant increases in the short life span of an individual insect with a narrow diet range. How plant chemistry and predation interact and their relative importances in the recurrent evolution of dietary specialization remains unknown.

Selection by both natural enemies and plant chemistry could in concert, result in a net narrowing of the herbivore's host range, providing that range limitation affords better protection. We wished to test the 'nasty host plant hypothesis' (hereafter ***nhph***), an hypothesis derived and modified from the parasitoid/insect host literature for application to the broader host plant/insect herbivory/predator reality of the Earth (from GUALD et al. 1992). At the micro-evolutionary time scale, ***nhph*** predicts that an insect will evolve a narrower diet, if, through the assimilation of the noxious compounds acquired from its host, it is rendered less vulnerable to its natural enemies. In macroevolutionary time, ***nhph*** also predicts that host shifts will always be to more, rather than less noxious plants. Specifically ***nhph*** predicts that, (1) when grown on the same host, the specialist should "handle", i.e. sequester, the host's chemistry better than the corresponding generalist does, both quantitatively and qualitatively; (2) specialists should fare better than generalists when subjected to natural predators in bioassays; (3) derived specialists will fare better than basal specialists do in bioassays, and finally; (4) derived specialists will have novel compounds in their defenses that account for the difference in efficacy.

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[1] Paper presented to the 6th International Symposium on the Chrysomelidae, Bonn, Germany, May 7, 2004.

While evidence exists both for (SMILEY et al. 1985; STAMP & BOWERS 1992; DYER & FLOYD 1993; MONTLLOR & BERNAYS 1993; METCALF 1994; DYER 1995; VENCL & MORTON 1998) and against ***nhph*** (STAMP 1992; RANK et. al. 1996; DOBLER et al. 1997; KÖPF et al. 1998; BECERRA & VENABLE 1999), a test of its ability to explain how narrow diets evolve, or to predict the direction of host shifts, is still lacking. Such a test would require a combinatorial approach that includes chemical, and mechanistic analyses, field ecology, within a framework of phylogenetically informed experiments (FUTUYMA 2000). The present study presents preliminary results from an ongoing research program underway in Panamá testing the specific predictions of ***nhph***.

Our study system, the larval tortoise beetle shield, is well suited for the investigation of how plant chemistry and predation might interact to favor the evolution of narrow diet breadths. Tortoise beetle larvae are soft-bodied, leaf surface grazers, and as such, are very apparent and predictable targets for predators and parasitoids. Their shields are composite structures formed from the exuviae and accumulated fecula (Fig. 1A). Shields are attached to a mobile infrastructure, the furca, which emanates from the tip of the abdomen (Fig. 1B). Tortoise beetle larvae possess a bizarre telescoping anus that serves to precisely deposit fecal material on the furca-exuvia complex (Fig. 1C). Shields can be aimed and rapidly waved in the path of an attacking enemy (Fig. 1D). In addition to being physical barriers, shields have been shown to contain a plant-derived, chemical component that significantly enhances their effectiveness as an anti-predator defense (GÓMEZ 1997; GÓMEZ et al. 1999; MÜLLER & HILKER 1999; VENCL et al. 1999). Shields are suitable for examining the host plant chemistry/predation interaction because they can be easily removed, chemically modified, and then reattached without otherwise harming the larvae (OLMSTEAD & DENNO 1993; VENCL et al. 1999).

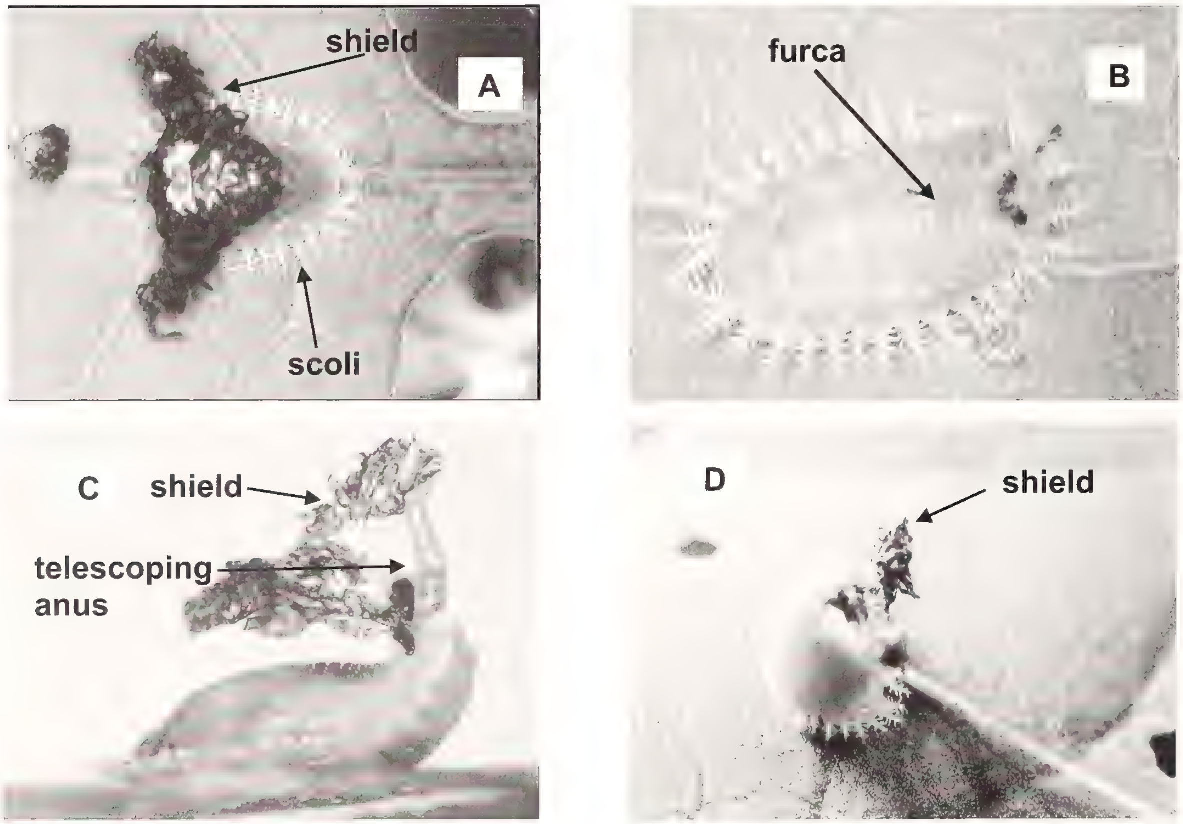

Fig. 1. Tortoise beetle larval shield system. (A) Dorsal aspect of shield (dark structure) and larval body with anterior oriented to the right. Scoli project laterally around the larval body and are probably sensory receptors. Three cast skins (exuviae) clearly visible within shield matrix; (B) De-shielded larvae with two-tined furca emanating from tip of abdomen and projecting above the larva; (C) Lateral view of larva with telescoping anus extended and applying fecula to shield; and (D) Shield tilted and waving in direction of perturbation (cat whisker) touching anterior end of larva.

Our objective was to test the predictions of ***nhph*** by examining the relative susceptibilities of generalist and of specialist tortoise beetle larvae to predation by a ubiquitous generalist ant predator, *Azteca,* in the Panamanian rain forest. We compared the effectiveness of shield defenses of three tortoise beetle species with contrasting diet ranges. To control for the potentially confounding effects of host plant chemistry on the behavior of predators, larvae of both diet-range types were reared on the specialist's host plant, members of the morning glory family, Convolvulaceae. We made two specialist-generalist dietary contrasts: (1) *Acromis sparsa*, a specialist on *Merremia umbellata,* against the generalist, *Chelymorpha alternans,* hereafter *Cm,* also reared on *M. umbellata* ; and (2) *Stolas plagiata,* a specialist on *Ipomoea phillomega,* once more against the generalist, *C. alternans,* hereafter *Cp,* also reared on *I. phillomega.* To address the importance of larval shield chemistry on ant behavior, shields of each species-host plant combination were subjected to micromanipulation and one of four leaching treatments prior to bioassay trials.

2. METHODS

Bioassays were conducted in Gamboa, Republic of Panamá, between 8:00 AM and 12:00 PM, during July, August, and September of 2003. *Azteca* ants (Hymenoptera: Formicidae: Dolichoderinae) are common, fierce, generalist predators in Neotropical lowland rainforests (CARROLL 1983; HÖLLDOBLER & WILSON 1990). We used *A. lacrymosa* as an assay agent. This species builds large carton nests attached to the boles of trees. They are extremely aggressive, strongly recruiting, and foraged primarily in the area in and around their home tree. One month prior to the onset of the bioassay experiments, we set potted individuals of *M. umbellata* and *I. phillomega* at the base of the home tree. Host vines were placed in contact with the tree trunks to enable the ants to use the host plants as foraging areas. We encouraged routine patrolling of *M. umbellata* and *I. phillomega* vines by the ants by regularly baiting host plant leaves with larva-sized tuna fragments.

Shield micromanipulation. Larval sibships of each species-host plant combination were equally divided at random among the following treatment groups: (1) water (H_2O); (2) methanol (MeOH); (3) both (H_2O followed by MeOH); and (4) unleached (intact) control. So that we could clearly observe the effects of diet range on shield chemistry in the absence of larval behavior, ant bioassay experiments were done using fourth-instar larvae freshly killed by freezing for 5 min. We immediately removed each larval shield by placing fine forceps between the tines of the furca and gently lifting the shield away from the body. Shields were then soaked for 25-30 min in a solvent bath agitated every five min (or two consecutive baths of 12-15 min each in the case of larvae assigned to the treatment with both H_2O and MeOH). After soaking, shields were dried on paper toweling under an incandescent light bulb and slow fan for 45 min. Each shield was re-attached to the larval furca using rapid-setting, fumeless, water-insoluble craft glue (DAP) that had been warmed to 28° C for five min to minimize setting time. Larvae with re-attached shields were allowed to stand and dry for at least 20 min before bioassays were begun. Controls consisted of the shield removal and reattachment manipulations, but no leaching.

To ensure high levels of ant activity on the host plants during bioassay trials, 45 min before the experiments began we baited each plant with pieces of tuna of about the same size as a fourth-instar larva. Each trial consisted of the presentation of an individual larva to foraging ants on either *M. umbellata* or *I. phillomega.* Initially, individuals from each treatment group were randomly assigned to different host plants with dice. Following the first round of testing the delegation of larvae to host plants was constrained by the previous round, such that no treatment group was tested on the same plant more than once nor tested consecutively. Only one trial was done on a given host plant before moving to the next tree, and a minimum of five min elapsed between each trial.

Using soft forceps, we placed each experimental larva near the center of a host plant leaf along the mid-vein. This formed the bioassay test arena. To avoid contamination, forceps were dedicated to a single treatment and were dipped in water and whipped to dryness between trials. A trial was started if there were at least two, but no more than five ants foraging on the leaf. Each trial lasted five minutes, or until the test larva was captured. A capture event was considered to be the movement of the test larva ≥ 1 cm toward the leaf petiole by the ants. Trials were recorded with a Panasonic digital video camera (PV-DV951) mounted on a tripod positioned such that the entire test leaf was included in the field of view. We started video recording at first contact of an ant with the experimental larva and measured the number of seconds elapsed between the start of the trial and a capture event (or the end of the trial period, whichever came first). Between 35 and 45 replicates of each solvent treatment were done for each of the four larval species-host plant combinations.

Statistical analyses. We examined the effects of larval diet range and shield chemistry on the time to capture by *Azteca* ants using failure-time statistics (PROC LIFETEST; SAS v. 9.0) (reviewed by FOX 2001). In contrast to classical methods such as ANOVA that compare either the total number of captures at the end of the experimental time interval or the mean time to capture among treatment groups, failure-time methods

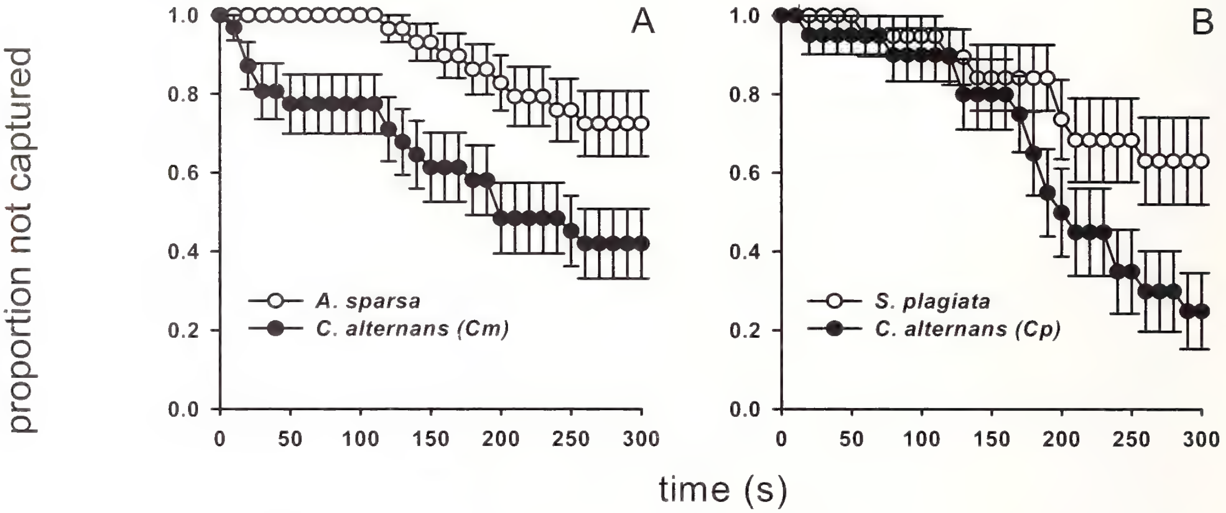

Fig. 2. Cumulative capture curves for specialist (open circles) and generalist (filled circles) tortoise beetle larvae with intact, unleached shields in Azteca ant bioassay. Larvae of both diet ranges were raised on either (A) *Merremia umbellata* (Contrast #1) or (B) *Ipomoea phillomega* (Contrast #2). Data points are the cumulative fraction of the cohort not yet captured (mean ±SE) for each 10 s interval in the bioassay. Both contrasts were statistically significant at the 0.05 level based on Bonferroni-corrected pairwise comparisons following a Wilcoxon signed-rank test for heterogeneity among all four groups ($P = 0.0040$).

compare the distributions of capture times over the entire experimental period. Times to the occurrence of a failure event (e.g., capture of a larva by ants) do not typically meet the distributional assumptions required by traditional parametric approaches. Such data often lack equal variances and normal distributions. In addition, many of the trials ended before a capture event was recorded (so-called right-censored data). As a consequence, the ultimate fate of the experimental larva beyond the 5 min census interval was unknown. Analysis of variance and related tests are unable to account for censored data, however, failure-time methods are not so limited. Cumulative capture functions were compared using a Wilcoxon signed rank test followed by pairwise multiple comparisons to determine specific differences between treatment groups (KALBFLEISCH & PRENTICE 1980). Significance levels were corrected using the sequential Bonferroni technique (Dunn-Sidák method; SOKAL & ROHLF 1995). This method is less conservative than the standard Bonferroni technique but ensures that an appropriate experiment-wise error rate is maintained.

Differences among groups in the proportion of larvae captured were assessed with likelihood-ratio chi-squared tests of independence (SOKAL & ROHLF 1995).

3. RESULTS

Failure-time analyses revealed pronounced differences between generalist and specialist larvae with both untreated and solvent-leached shields in susceptibility to predation by *Azteca* ants. The relative performance through time of generalists and specialists with untreated shields is shown in Figure 2. In both diet range contrasts, the specialists were consistently less susceptible to predation than were generalist larvae. Specialist larvae were also significantly less likely than generalists to have been captured by the end of a trial (Contrast #1: $G^2 = 5.78$, $P = 0.016$, Contrast #2: $G^2 = 5.92$, $P = 0.015$).

Tortoise beetle shield chemistry. The effects of solvent leaching of shields on larval susceptibility to predation were striking. In both contrasts, regardless of diet range, the decay in capture curves for shields leached by some or all solvents (H_2O, MeOH or both) was significantly steeper than in curves for intact, unleached shields (Figs 3 and 4; Table 1). For both specialists, shield leaching by H_2O had stronger effects on larval capture rates than leaching by MeOH. In contrast, there appears to be an interaction in the effects of different solvents on shields of generalist larvae (although our experimental design unfortunately does not allow for a statistical test of this possibility). Leaching by MeOH had a larger (negative) effect than leaching by H_2O on capture rates of *C. alternans* grown on *Merremia umbellata* (Contrast #1) compared to untreated controls. However, the opposite pattern exists for *C. alternans* grown on *Ipomoea phillomega* (Contrast #2) (Figs. 3 and 4; Table 1).

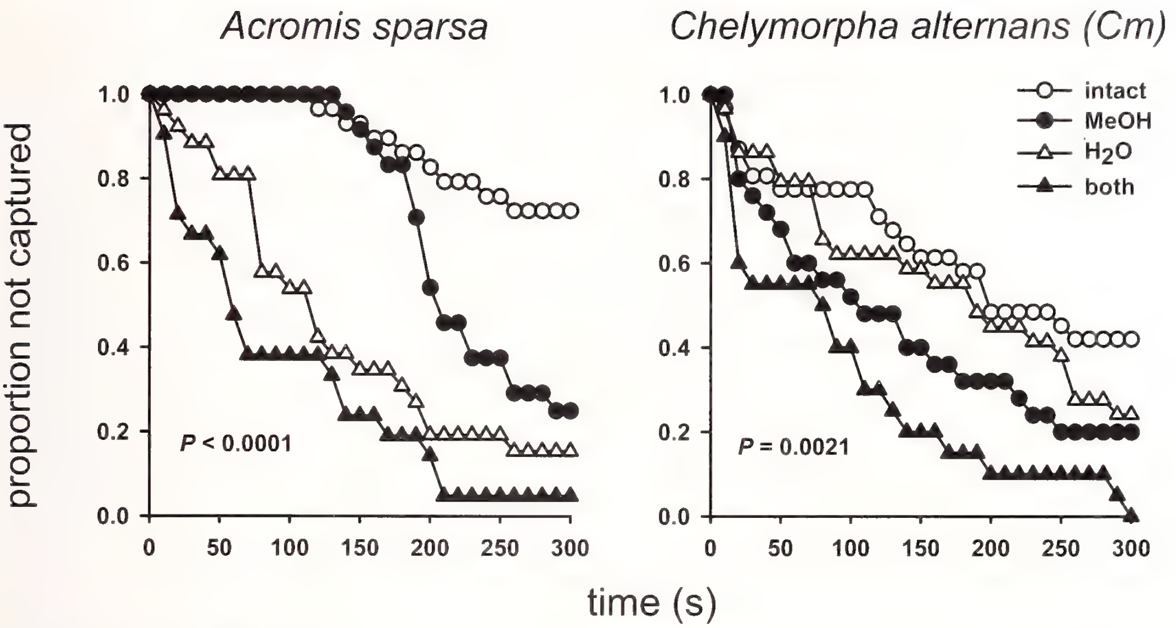

Fig. 3. Cumulative capture functions for specialist (*A. sparsa*) and generalist (*C. alternans, Cm*) tortoise beetle larvae raised on *Merremia umbellata* (Contrast #1) with intact and solvent-leached shields in the *Azteca* ant bioassay. *P*-values are from a Wilcoxon signed-rank test for heterogeneity among groups. Statistical results of Bonferroni-corrected pairwise comparisons are presented in Table 1. Error bars were eliminated for clarity.

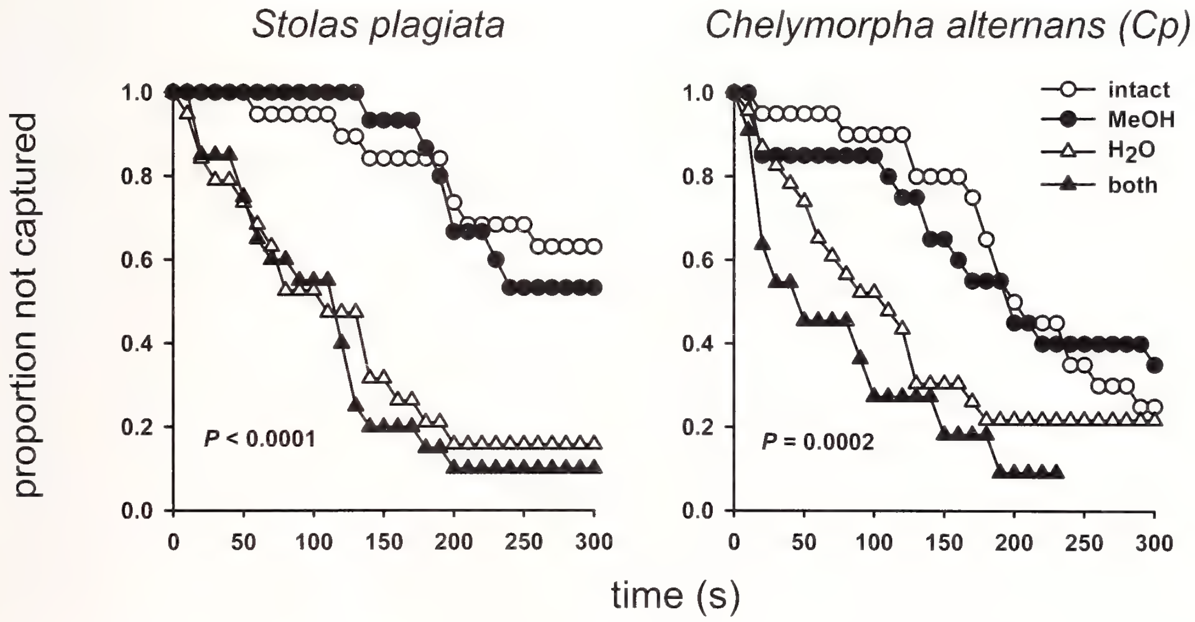

Fig. 4. Cumulative capture functions for specialist (*S. plagiata*) and generalist (*C. alternans, Cp*) tortoise beetle larvae raised on *Ipomoea phillomega* (Contrast #2) with intact and solvent-leached shields in the *Azteca* ant bioassay. *P*-values are from a Wilcoxon signed-rank test for heterogeneity among groups. Statistical results of Bonferroni-corrected pairwise comparisons are presented in Table 1. Error bars were eliminated for clarity.

Table 1. Pairwise multiple comparisons of cumulative capture curves for specialist (*A. sparsa* and *S. plagiata*) and generalist (*C. alternans*) tortoise beetle larvae with intact and solvent-leached shields in the *Azteca* ant bioassay (Figs 3 and 4). Larvae of both diet ranges were raised on either *Merremia umbellata* (Contrast #1) or *Ipomoea phillomega* (Contrast #2). To keep the experiment-wise error rate at the 0.05 level, comparisons were done using a sequential Bonferroni approach (Dunn-Sidák method; Sokal and Rohlf 1995) following Wilcoxon signed-rank tests. Individual comparisons marked with an asterisk (*) were statistically significant.

	Contrast #1		**Contrast #2**	
Shield type	***A. sparsa***	***Cm***	***S. plagiata***	***Cp***
intact v. MeOH	*	*ns*	*ns*	*ns*
intact v. H_2O	*	*ns*	*	*
intact v. both	*	*	*	*
MeOH v. H_2O	*	*ns*	*	*
MeOH v. both	*	*ns*	*	*
H_2O v. both	*ns*	*	*ns*	*ns*

4. DISCUSSION

4.1. Are specialists better defended than generalists?

Our findings support the central tenet of ***nhph***, the 'nasty host plant hypothesis', which posits that when both are feeding on the same host plant, specialist tortoise beetle larvae will be better defended against predation by their shields than are generalist larvae in an ant bioassay. We found that specialists with unleached, intact shields clearly outperformed their generalist counterparts in both diet contrasts we tested. Furthermore in both contrasts, we observed that all solvent leaching treatments (H_2O, MeOH, and both) significantly degraded shield effectiveness, regardless of diet range. This latter finding supports the idea that shields have a critically important chemical component that consists of both polar and non-polar compounds.

4.2. Is the chemical defense derived from the host plant?

Although a definitive answer to the question of the provenance of shield compounds must await comparisons of plant and shield chemistries, evidence from this study supports the idea that shields are fortified with host-derived metabolites. If a shield system were based on autogenous synthesis, shield chemistry would be the same regardless of diet and thus one would not expect to observe differences in shield performance. When we compared the shield performances of the same beetle, *C. alternans*, reared on different host plants, we observed that effect of a particular leaching treatment depends on which plant the generalist fed upon, supporting the idea that at least part of larval shield chemistry is host-derived. In all the other fecal shield-bearing species, including several tortoise beetles studied so far, shield chemistry is based on precursors obtained from the host plant (GÓMEZ 1997; MORTON & VENCL 1998; VENCL & MORTON 1998; MÜLLER & HILKER 1999). Fecula-laced shields may well represent a type of sequestered defense. If their chemical constituents were found to be host-derived, the shields of the tortoise beetles in this study would also strongly resemble sequestering types of defenses.

4.3. Do specialists sequester host chemistry better than generalists?

Our findings lend support to the ***nhph*** prediction that specialists are more competent than are their generalist counterparts at handling host plant chemistry. Our data show that the H_2O leaching treatment, which removed many of the more polar compounds from the larval shields, significantly increased the susceptibility of both specialist larvae to predation. In contrast, the MeOH leaching treatment had a greater impact on the generalist feeding on one host but not the other. Superior chemical sequestration might involve one or more of the following strategies: greater bio-concentration of a particular compound, differential sequestration of a variety of compounds, or the modification of the compounds.

Many specialist herbivores are known to have enhanced mechanisms for the sequestration and/or the transformation of plant metabolites into defensive compounds (BOWERS 1988; PASTEELS et al. 1983, 1988; DENNO et al. 1990). Some specialist herbivores have been found to more efficiently excrete or egest host plant secondary compounds (SELF et al. 1964; BERENBAUM 1983; FERGUSON et al. 1985; METCALF 1994). We think that the tortoise beetle shield system is a type of sequestration process that is relatively inexpensive (OLMSTEAD & DENNO 1993), possibly because tortoise beetle specialists are superior at harvesting and modifying host metabolites compared to their generalist counterparts feeding on the same hosts.

Since they cannot readily transit cell membranes, nonpolar compounds are arguably more difficult to manipulate because they first must be modified in order to contain them within the larval gut (DUFFY 1980). The process of gut compartmentalization requires that a compound be made more polar through mechanisms like hydroxylation or conjugation (DUFFY 1980; BOWERS 1988). Our data suggest that given identical dietary inputs, specialists are more competent at transforming less polar into more polar compounds, and thus disproportionately fortifying their fecula with more polar compounds, compared to their generalist counterparts. The identity and defensive characteristics of these more polar shield constituents must await future structural elucidation. Suffice it to say that many classes of polar substances are well known to have deterrent and toxic characteristics. Some of these more polar compound classes include pyrrolizidine alkaloids, phenolics, cardenolides, sapogenines, and flavonoids.

4.4. Adaptation or accident?

How herbivorous insects use their host plants for chemical defense, i.e., by processes of sequestration, may entail quite different physiological mechanisms from those used by tortoise beetles for processing host compounds into shield fecula. Does shield formation require special adaptations or are shields passive consequences of host consumption? Based on findings from shield-forming leaf beetles in other chrysomelid subfamilies, VENCL & MORTON (1998) have suggested that shields are not 'default' waste tanks, but instead are adaptations for defense. They argue that since shields contain a highly culled subset of ingested host derived precursors, some of which are nutrients and some of which are modified within the larval gut, fecal shield formation must have entailed the evolution of specialized enzymes that now serve the triple defensive functions of: (1) selective compound egestion through compartmentalization, (2) compound bio-concentration, and (3) compound bio-activation (VENCL et al. 1999). The unusual telescoping anus of tortoise beetles is *de facto* evidence of a specialized adaptation for the precise deposition of fecula on the shield framework (see Fig. 1B). There is good evidence from another tortoise beetle, *Plagiometriona clavata,* supporting the contention that shields with fecular retention represent specialized adaptations for predator defense (VENCL et al. 1999). For example, palmitic acid is one of the 'discarded' compounds that eventually ends up in *P. clavata's* shield. An erstwhile nutrient, it occurs in the fecula in relatively higher concentrations than it does in the host. Palmitic acid also elicits necrophoresis (undertaker behavior) in ants, whereby anything emitting it gets placed on the ant nest's dump (BLUM 1970). Palmitic acid therefore appears to be more beneficial as part of the larval defense system than as a dietary nutrient.

Our findings for tortoise beetles are the first instances where specialists have been shown to derive an advantage (enemy-free space) over their respective generalists when reared on the specialist's host plant. This conclusion is in overall agreement with previous studies on Lepidoptera (STAMP & BOWERS 1992; DYER & FLOYD 1993; CORNELIUS & BERNAYS 1995, but see STAMP 1992). It is important to note that the Lepidoptera and herbivorous Coleoptera represent well over half the insects attacking plants and most of these herbivores are dietary specialists (STRONG et al. 1984). More work is necessary to determine if the relationship between the effectiveness of plant-derived, anti-predator chemical defenses and specialization is a general one that has influenced the evolution of diet range in beetles and possibly in other phytophagous insects.

We are in the process of determining the origins and elucidating the chemical structures of the compounds responsible for the effects observed in this study. At a macroevolutionary level, ***nhph*** predicts that derived specialists will have novel, more polar compounds in their defenses that account for increased shield efficacy when compared to generalists or to basal specialists. If so, then the remarkably robust tortoise beetle radiation might have been fostered by the colonization of increasingly more chemically complex dicotyledonous plants. A process of defensive escalation may have enhanced the likelihood of beetle speciation. Whether host shifts have always been to plants containing more, rather than less potent chemistry must await further studies of more basal specialists and generalists in the tortoise beetle radiation. It is also essential to determine if selection on shield chemistry is diffuse, or whether each predator's selective impact is idiosyncratic, in which case, we would expect specificity in targeting of particular shield chemicals. We are currently undertaking studies to clarify these related issues.

Acknowledgements. We wish to thank Kamal Kamalrage, Anayansi Valderrama, Jessica Gurevich, Donald Windsor and Gordon Fox for their help, encouragement, and thoughtful suggestions. We want to thank Fumio Aoki for his invaluable assistance. This is contribution # 1123 from the Graduate Program in Ecology and Evolution at Stony Brook University. This study was funded by NSF IBN # 108213 to the senior author.

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Bonner zoologische Beiträge	Band 54 (2005)	Heft 4	Seiten 297–303	Bonn, Oktober 2006

On Phyletic Closeness Between South American and New Caledonian Spilopyrines (Chrysomelidae, Eumolpinae, Tribe Spilopyrini)[1]

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Abstract. Among members of the eumolpine tribe Spilopyrini (Reid 1995), the South American genera *Hornius* and *Stenomela* and the New Caledonian *Bohumiljania* are especially similar, while the Australian and the New Guinean forms seem to stand a little apart. In this communication, by tracing taxonomic history of spilopyrines, and by taking into account their food plants, palaeogeological history of the Southern Hemisphere, anatomical features of spilopyrines, and their developmental stages, a possible phyletic closeness between the South American and the New Caledonian genera has been inferred.

Key words. Taxonomy, ecology, zoogeography

1. INTRODUCTION

REID (2000) separated some members of the chrysomelid subfamily Eumolpinae, and put them in a new subfamily, Spilopyrinae. Earlier these genera had been regarded by REID (1995) as a tribe under Eumolpinae, the Tribe Spilopyrini. These primitive Eumolpinae are being referred to in this communication as spilopyrines, following VERMA & JOLIVET (2004). The spilopyrin genera include: *Spilopyra* Baly, 1860 (Australia and New Guinea), *Macrolema* Baly, 1861 (Australia and New Guinea), *Richmondia* Jacoby, 1898 (Australia), *Cheiloxena* Baly, 1860 (Australia), *Stenomela* Erichson, 1847 (Chile), *Hornius* Fairmaire, 1848 (Chile and Argentina), and *Bohumiljania* Monrós, 1958 (New Caledonia). As pointed out by VERMA & JOLIVET (2004), the Chilean and the New Caledonian spilopyrines are especially similar. This communication aims to emphasize a possible phyletic closeness between the South American and the New Caledonian spilopyrines. In this context the following are specifically notable.

2. TAXONOMIC HISTORY

JOLIVET (1954), describing the wing venation in the New Caledonian spilopyrin, referred to it as *Stenomela caledonica*. MONRÓS (1958) created a new generic name for this spilopyrin, *Bohumiljania*. SEENO & WILCOX (1982), following MONRÓS (1958), placed *Stenomela* and the New Caledonian *Bohumiljania* together under the Tribe Stenomelini, a tribe under Eumolpinae. The Tribe Hornibiini, with a single genus *Hornius*, has been placed close to the Tribe Stenomelini. These bits of taxonomic history clearly support the notion of phyletic closeness between the S. American and the New Caledonian forms.

3. FOOD PLANTS

Hornius of Chile, as larva and adult, is a specialised feeder on leaves and bark of *Nothofagus* trees (Fagaceae) (JEREZ 1996). *Stenomela* of the same region, on the other hand feeds on different species of Myrtaceae (*Blepharocalyx crukshanksii* Niedenzu and *Luma* spp.). *Bohumiljania caledonica* in the distant New Caledonia, also feeds on Myrtaceae (*Sizygium* spp.). This is a point of similarity between *Stenomela* and *Bohumiljania*. But in spilopyrines, *Cheiloxena* in Australia also feeds on Myrtaceae (*Eucalyptus* spp.) and *Spilopyra* on Sapindaceae (*Cupaniopsis* and *Guioa*). Host plants of *Macrolema* and *Richmondia* are not on record (JOLIVET et al. 2003).

4. PALAEOGEOLOGICAL HISTORY

In the context of distribution of spilopyrines, the Gondwana Hypothesis has been invoked by JEREZ (1996) and REID (2000). HOLLOWAY (1979) and VERMA & JOLIVET (2004) have pointed out that in the late Cretaceous (75 mya) continental shelves of S. America and of the Australian Plate were still connected with those of the Antarctica, while Africa and India, that also resulted from the break, had moved away northward considerably removed from Gondwanaland.

In a recent paper SANMARTIN & RONQUIST (2004) gave a detailed and interesting account of Gondwanian history, supported by explicit maps of the southern hemisphere in different geological periods. The following parts of the history, as mentioned in that paper

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[1] Paper presented to the 6th International Symposium on the Chrysomelidae, Bonn, Germany, May 7, 2004.

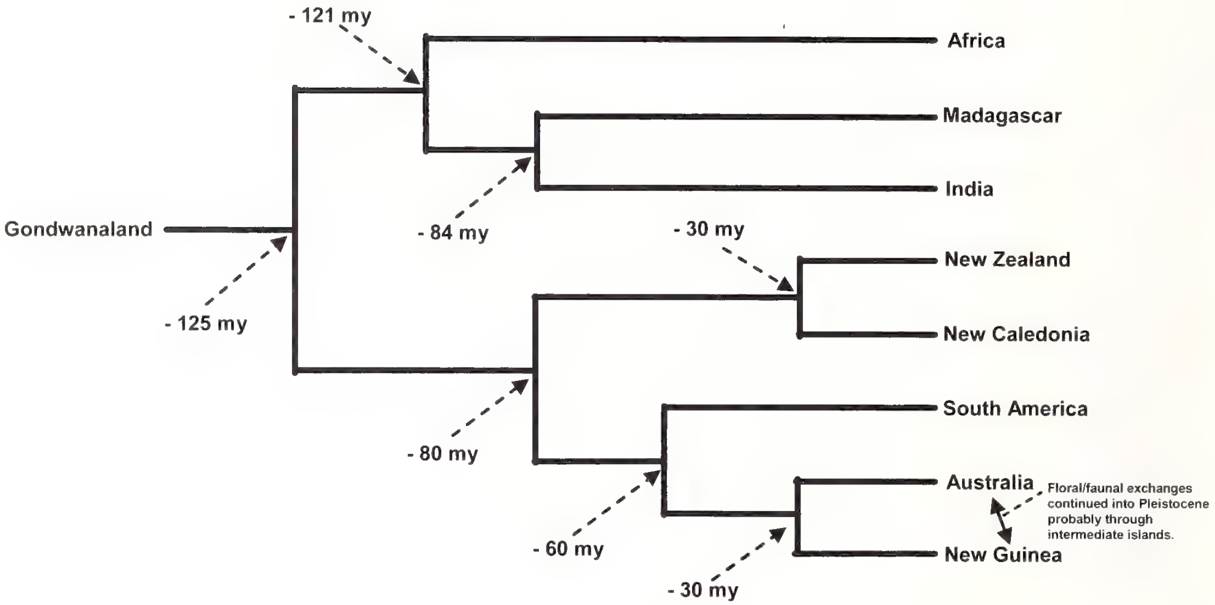


Fig. 1. Cladograms showing sequence of separation of land masses in the Southern Hemisphere (based on data in SANMARTIN & RONQUIST 2004, and in a summary of her studies provided by I. Sanmartin, Uppsala, pers. comm. 2004).

and in a summary of their work, provided by Isabel Sanmartin (Uppsala, pers. comm. 2004), are of special interest in the present context.

(i) "Consistent with other studies, the animal data are congruent with the geological sequence of Gondwana breakup……Trans-Antarctic dispersal (Australia ←→ southern South America) is also significantly more frequent than any other dispersal event in animals, which may be explained by the long period of geological contact between Australia and South America via Antarctica." (SANMARTIN & RONQUIST 2004).

(ii) In Palaeocene (60 mya) New Zealand + New Caledonia separated from Australia.

(iii) In mid to late Tertiary (mid Tertiary 40 to 30 mya) New Caledonia separated from New Zealand.

(iv) During the period 60 to 30 mya Australia and South America remained in contact across Antarctica (Fig. 5), and this continued up to Eocene-early Miocene. At this time the Antarctica had a warm temperate climate, and had a rich flora, dominated by *Nothofagus*, as evidenced by fossils of this plant found in coastal parts of the Antarctica. Ready dispersal of *Nothofagus* to Australia and South America is probable. I. Sanmartin (Uppsala, pers. comm. 2004) points out, "This (= a warm temperate climate in the Antarctica) presumably established a significant dispersal route for the exchange of southern temperate biota between South America and Australia"

(v) Opening of the Drake passage between Antarctica and South America at the boundary between Eocene and Oligocene (30 to 28 mya led to the onset of the Circum-Antarctic Current, and this resulted in cooling of the Antarctica.

JEREZ (1996) has pointed out that *Nothofagus* arose in the Australian part of Gondwana, and from there it dispersed to New Zealand and S. America.

As mentioned above, *Hornius* is a specialized feeder on *Nothofagus*. It appears that primitive spilopyrines dispersed to Australia, New Caledonia and S. America, along with temperate flora, like *Nothofagus*, and subsequently, due to cooling and development of subantarctic conditions in the southern part of S. America, and due to separation of New Caledonia as an island from the Australian Plate, the primitive spilopyrines in these parts became shielded from competition with more modern forms, and have survived as *Hornius* and *Stenomela* in southern S. America, and as *Bohumiljania* in New Caledonia. One may ask: New Guinea is also an island, and it shares *Spilopyra* and *Macrolema* with Australia, then how island isolation of New Caledonia could help the survival of *Bohumiljania* as a primitive spilopyrin? One answer to this question: New Zealand + New Caledonia separated from Australia in Palaeocene (60 mya), whereas floral and faunal exchanges between Australia and New Guinea could continue even into the Pleistocene (I. Sanmartin, Uppsala, pers. comm., 2004) (Fig. 5).

5. ANATOMICAL FEATURES

New Caledonian and S. American spilopyrines have an elongated and cerambycid like body shape (Fig. 2). The Australo-Papuan genera in contrast have a more compact and robust body form like typical Eumolpinae. All the three S. American-New Caledonian genera are light green in colour on the host plant. On the other hand the Australian genera show bright and diverse metallic colours.

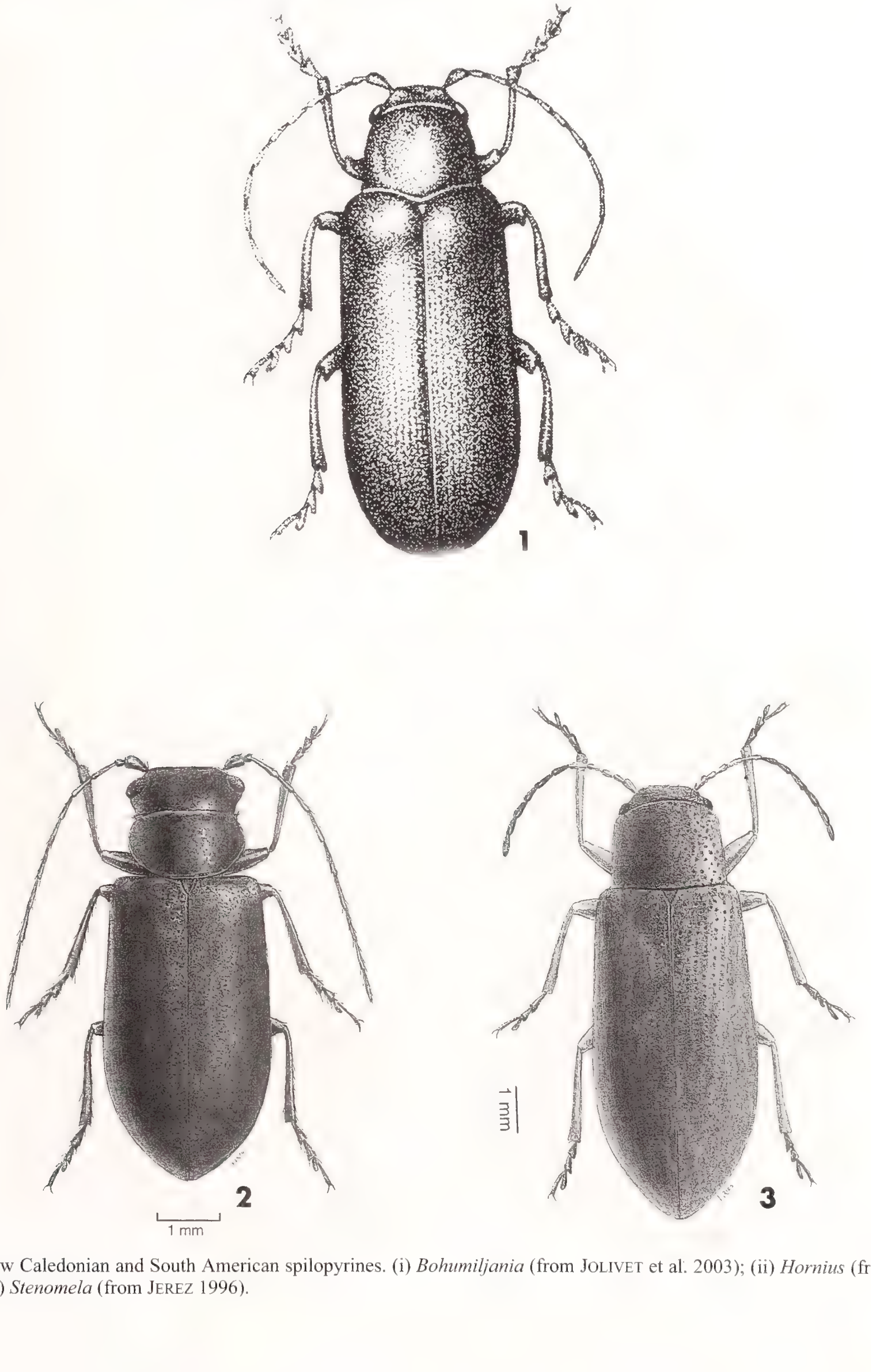


Fig. 2. New Caledonian and South American spilopyrines. (i) *Bohumiljania* (from JOLIVET et al. 2003); (ii) *Hornius* (from JEREZ 1996); (iii) *Stenomela* (from JEREZ 1996).

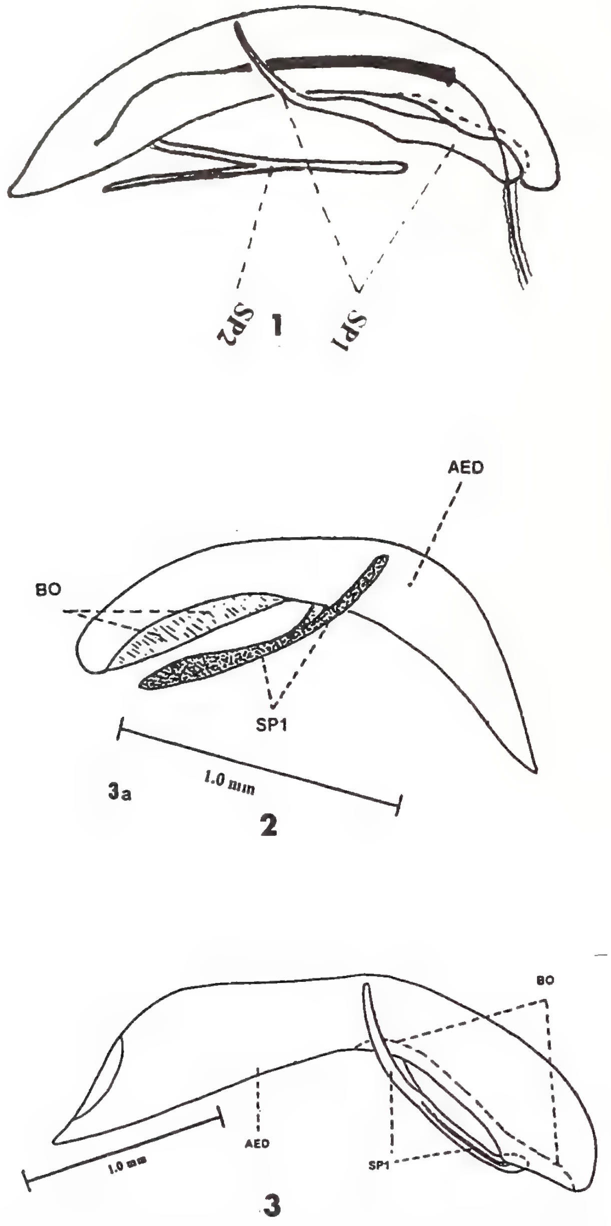


Fig. 3. Aedeagi, lateral view. (i) of *Bohumiljania*; (ii) of *Hornius*; (iii) of *Stenomela* (from VERMA & JOLIVET 2004).

The aedeagal structure in spilopyrines in general is primitive, as discussed by VERMA & JOLIVET (2004). But in *Hornius*, *Stenomela* and *Bohumuljania* it is even more primitive; the primitive features of their aedeagi include:

(i) Poor differentiation of the basal hood and the aedeagus proper (Fig. 3).

(ii) Only moderate ventral curvature of the aedeagus, spread throughout the length of the organ, and not confined to the basal part of the aedeagus proper. In *Stenomela*, however the curvature is more marked in the basal part of the aedeagus proper.

(iii) The ventrally directed basal orifice of the aedeagus is relatively restricted anteroposteriorly.

In contrast: (i) In *Spilopyra, Macrolema, Cheiloxena* and *Richmondia* the differentiation of the basal hood and the aedeagus proper is somewhat better marked than in the S. American and New Caledonian forms; (ii) In *Richmondia, Cheiloxena* and to some extent in *Spilopyra* the ventral curvature of the aedeagal tube is more marked than in S. American and New Caledonian spilopyrines, and in *Richmondia* and *Cheiloxena* this curvature is almost as strong as in higher Eumolpinae; and (iii) the anteroposterior extent of the basal orifice is large, specially in *Macrolema*, *Cheiloxena* and *Richmondia* (For differences between typical eumolpine and spilopyrin aedeagi see VERMA & JOLIVET 2004).

Thus the aedeagal structure in *Hornius, Stenomela* and *Bohumiljania* is more primitive than in the remaining spilopyrines, and almost of the chrysomeline type (For features of the chrysomeline type of aedeagus see VERMA 1996).

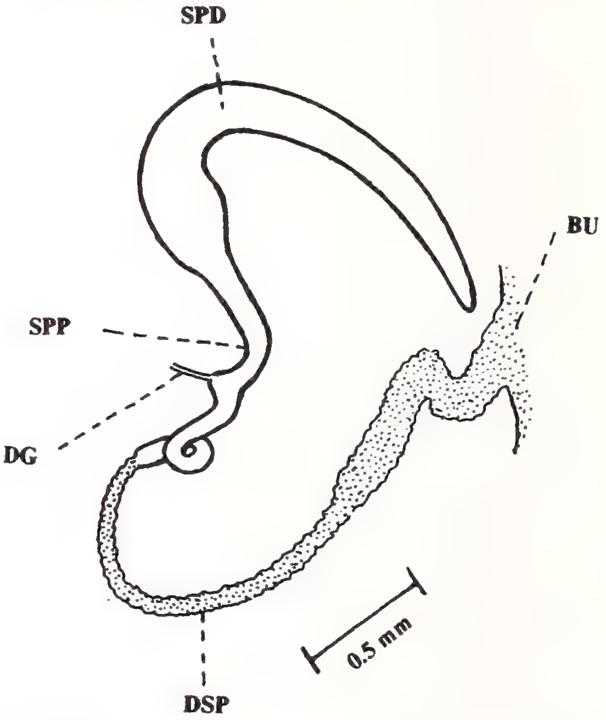
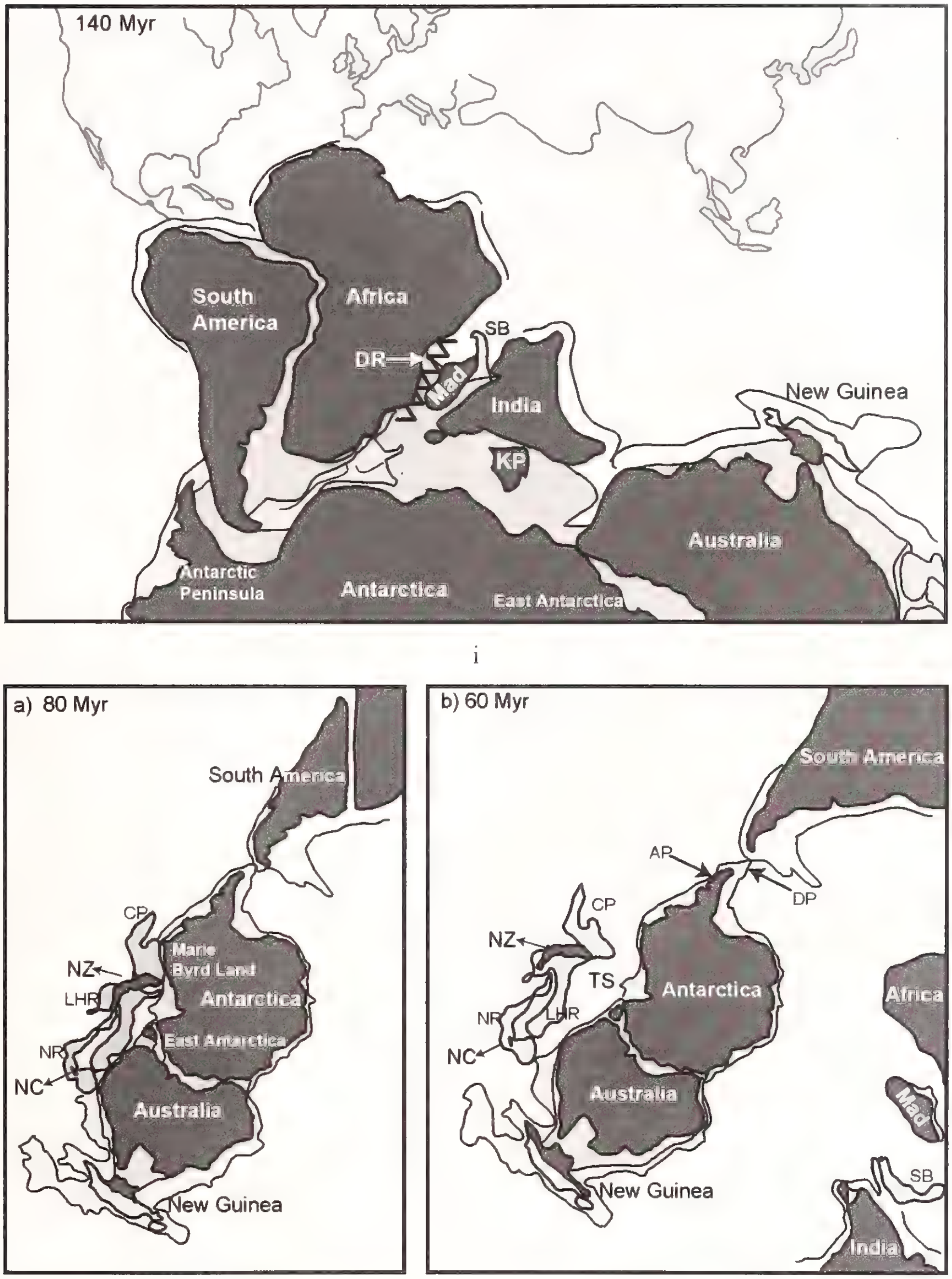


Fig. 4. Spermathecal complex of *Bohumiljania* (from VERMA & JOLIVET 2004).

Spermatheca in all spilopyrines shows a characteristic eumolpine feature, namely the proximal part of the spermathecal capsule is differentiated into a swollen or bulbous section, which receives the duct of the spermathecal gland and from which the spermathecal duct starts. In *Bohumiljania* this proximal part is somewhat elongated and presents some irregular coiling (Fig. 4). Such a coiling is seen also in the spermatheca of


140 Myr
South America
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a) 80 Myr
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Marie Byrd Land
Antarctica
LHR
East Antarctica
NR
NC
Australia
New Guinea
b) 60 Myr
South America
AP
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SB
New Guinea
India

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ii iii

Fig. 5. Southern hemisphere. (i) Gondwana (-140 my). End of Jurassic; (ii) Polar view of the Southern hemisphere (-80 my). Mid-Cretaceous; (iii) Polar view of the Southern hemisphere (- 60 my). Early Eocene. The Drake Passage is just forming. New Zealand, New Caledonia, Norfolk ridge and Lord Howe ridge are also figured (from Isabel Sanmartin summary (2002), pers. comm. 2004, with permission).

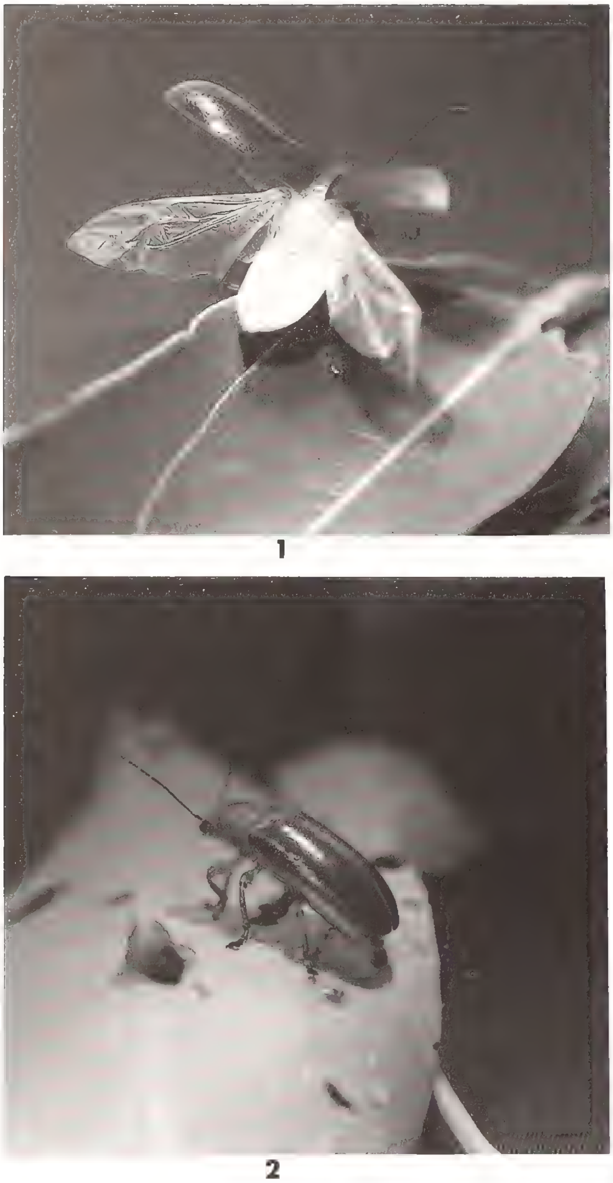

Fig. 6. *Bohumiljania caledonica* (Jolivet). (1) starting to fly; (2) on a *Syzygium cumini* L. (Myrtaceae) leaf, in New Caledonia

Megascelinae (SUZUKI 1988). Megascelinae are essentially Central and South American in distribution, and are closely related to Eumolpinae (JOLIVET 1957-1959; REID 1995; COX 1998). Should this situation be regarded as covered by what has been described by MAYR & ASHLOCK (1991) in the following part of their text? "A serious problem is posed by propensity of genotypes to produce a certain phenotype, such as stalked eyes in certain acalyptrate dipterans, which is manifested in only some of the possessors of a genotype. Parallelism in this case may be defined as homologous similarity, since the common ancestor evidently had the genetic propensity even if it was not expressed phenotypically." In this context it would be relevant to point out that *Megascelis* does not have a mediocubital patch in the hind wing like spilopyrines. *Richmondia*, however has a dark spot in this position, and not a well defined mediocubital patch (VERMA & JOLIVET 2004).

6. DEVELOPMENTAL STAGES

Eggs of *Hornius* are laid under an oothecal cover, made of excrement material, and a single cover includes 7-8 eggs (JEREZ & CERDA 1988). In *Stenomela,* eggs are also provided with excretory matter cover, each cover protecting two eggs. In *Bohumiljania* the ootheca is made up of excretory material mixed with vegetal fibres and a glandular secretion, and there are four eggs per ootheca (JOLIVET et al. 2003). Perhaps it will not be out place to mention that in *Megascelis* there is also a membranous protective cover for a batch of about 10 eggs (COX 1988). In remaining spilopyrines laid eggs have not yet been observed and reported.

The neonate larva of *Bohumiljania* bores onto the stem of the host plant, but later instars are exposed feeders on leaf lamina (JOLIVET et al. 2003). There is a similar habit with the first instar larvae of *Hornius* and *Stenomela*; they pierce into leaf buds and leaf lamina, but later instars are well exposed, feeding on leaves. Larval habits have not been recorded so far for the Australian spilopyrines.

Pupae of *Hornius* are formed in soil in a specially constructed cell (JEREZ 1996). Pupae of *Stenomela* and *Bohumiljania* have not been observed yet, but they too are believed to be formed in soil (JEREZ 1995; JOLIVET et al. 2003).

7. CONCLUDING REMARKS

Phyletic closeness between spilopyrines of New Caledonia and S. America has been hypothesized on the basis of the above discussion. This hypothesis will hopefully gain additional support through further studies on the biology of the Australian spilopyrines, and through DNA analysis studies.

Acknowledgements. We must thank here Dr. Michael Schmitt, from Zoologisches Forschungsmuseum Alexander Koenig, Bonn, who welcomed the junior author at the Chrysomelid symposium held during the African Biodiversity Conference, in May 2004, and Dr. Michael Thomas, from the Florida Museum of Entomology, Gainesville, FL who has provided laboratory access to the junior author while in the USA. Our best thanks also to Dr. Isabel Sanmartin (Uppsala University, Sweden) who provided decumentation and illustrations.

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Bonner zoologische Beiträge	Band 54 (2005)	Heft 4	Seiten 305–312	Bonn, Oktober 2006

Species Composition of Leaf Beetle Assemblages in Deciduous Tree Canopies in Hungary (Coleoptera: Chrysomelidae)[1]

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Abstract. The species richness and species composition of Coleoptera assemblages were investigated in deciduous tree canopies in Hungary. Apple and pear orchards were investigated in Nagykovácsi, Kecskemét and Sárospatak in 1990–94, and limes and maples in Keszthely in 1999–2002. This study presents in detail the findings on leaf beetles.

Earlier investigations in Hungary revealed surprisingly high diversity of Coleoptera assemblages in the canopy of apple and pear orchards. Altogether 324 species, almost 3 per cent of Hungary's beetle fauna, were represented: 253 in apple and 188 in pear orchards. The majority of the species belonged to the Curculionidae, Chrysomelidae and Coccinelidae families. The proportion of leaf beetles ranged between 15 and 20 %. The commonest leaf-beetle species in the canopy of the commercial orchards investigated were *Phyllotreta vittula*, *Phyllotreta atra*, *Phyllotreta nigripes*, *Oulema melanopus*, and *Aphthona euphorbiae*. In the abandoned orchards, the commonest were *Luperus xanthopoda*, *Smaragdina salicina* and *Orsodacne lineola*.

Examination of the fauna of parks, avenues and other planted urban plant stocks has only begun to occupy researchers in the last decade. Analysis of the full Arthropoda assemblages of these plant stocks has still not been undertaken. The proportion of leaf-beetle species in the material gathered on maples and limes in Keszthely ranged between 17.0 and 21.3 per cent. Apart form leaf beetles, the bulk of the specimen material collected consisted of species of the Coccinellidae, Staphylinidae and Curculionidae families. The commonest leaf-beetle specimens collected in the lime canopy were *Aphthona euphorbiae, Chaetocnema tibialis, Longitarsus lycopi, Longitarsus pellucidus, Longitarsus pratensis* and *Longitarsus succineus*. The commonest on maple were *Aphthona euphorbiae, Chaetocnema concinna, Chaetocnema tibialis, Longitarsus lycopi, Longitarsus pellucidus, Longitarsus succineus, Phyllotreta cruciferae* and *Phyllotreta vittula*.

It was concluded that leaf beetles contribute a high proportion of the biodiversity of the deciduous tree canopy, sometimes occurring with high species richness and abundance. However, the reasons for this occurrence and their potential role are poorly understood.

Key words. Coleoptera, Chrysomelidae, Hungary, faunistics, deciduous tree canopy fauna

1. INTRODUCTION

Attention focused on apple and pear orchards during the development of integrated plant-protection methods. Knowledge of the biology of some key pests and predators (BALÁZS 1992; BLOMMERS 1994; HERARD 1986) is extensive enough to describe the role of these organisms in the ecological processes of such orchards. Yet the species composition and diversity of the total arthropod assemblages are still poorly known, although the information could be essential to a general understanding of the biodiversity relations of the plantations.

Two long-term investigations of the arthropod fauna of apple orchards in Hungary have been carried out in the last century (ZILAHI-SEBESS 1955; MÉSZÁROS 1984). An additional investigation focused on the Coleoptera assemblages of apple and pear orchards in Hungary (MARKÓ et al. 1995).

Examination of the fauna of parks, avenues and other planted urban plant stocks has only begun to occupy researchers in the last decade. This research had several objectives, but plant-protection criteria were dominant. Nonetheless, analysis of the full Arthropoda assemblages of these plant stocks has still not been undertaken.

This study aims to compare the leaf-beetle samples collected in the canopy of deciduous trees in Hungary and explain the similarities and differences between the samples.

2. MATERIALS AND METHODS

Investigations of the canopy fauna of apple and pear orchards were carried out in three geographical regions of Hungary. The samples were collected at the following localities. Nagykovácsi (3 plots) is situated in the centre of Hungary in woodland amidst hills of medium height and surrounded by mixed oak forest. Kecskemét (5 plots), situated in the Great Hungarian Plain, and Sárospatak (4 plots) in Northern Hungary both lie in a lowland agricultural environment. Some of the selected plots had been untreated, and others treated with broad-spectrum insecticides (mainly organophosphorus insecticides and pyrethroids), and also treated with selective insecticides (mainly IGR pesticides) in IPM orchards. The samples restricted to the canopies were collected between 1990 and 1994, from April to November, by beating methods, using the Winkler-type umbrella (Ø 0.7 m) or 0.25 m^2 plastic sheet. Sampling per year varied between 12 and 22 occasions. The number of trees per sampling varied between 10 to 30. Table 1 shows the parameters of each area investigated.

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[1] Paper presented to the 6th International Symposium on the Chrysomelidae, Bonn, Germany, May 7, 2004.

Table 1. Description of the orchards investigated in Hungary (after Markó et al. 1995)

	Woodland in hill of medium height			**Agricultural lowland**			
	Nagykovácsi			Kecskemét			Sárospatak
Fruit species	apple	pear	pear	apple	apple	apple	pear
Age of plantation	M	M	M	Y	Y	M	M
Size of plantation	5.8 ha	1.1 ha	51 ha	2 ha	2 ha	5–6 ha	50.6 ha
Untreated	+	+					
Conventionally treated			+	+	+	+	+
IPM applied				+	+	+	+
No. of treatments	–	–	3–6	7–8	7–8	7–8	7–8
Collecting method	U	U	U	U	S	U	U
Years	1990–92	1992–4	1992–4	1992–3	1992–4	1992–4	1993–4
Sampling per year	12	12	12	12	23–24	21–22	4/1993 7/1994
Trees per sampling	10	10	12	10	30 branches	10	10

M = mature tree, more than 13 years old; Y = younger than 13 years old; U = umbrella; S = plastic sheet

Investigation of lime and maple canopies was carried out in Keszthely and vicinity in 1999–2002. Keszthely lies in the middle of Western Hungary at the western end of Lake Balaton, in a basically agricultural lowland environment. Collections were made 8–10 times during the vegetation period, using pyrethroid spraying of the whole canopy and canopy netting (Ø = 0.5 m). The number of trees per sampling varied between 4 to 10.

The composition of the chrysomelid communities was compared by metric ordination (principal coordinate analysis—PCoA), based on the Horn index, after log2 transformation of the data, and the Jaccard similarity index (Krebs 1989), using the Syntax 5.1 program (Podani 1997). The starting data for these analyses were obtained by aggregating all the individuals collected in the canopy of the orchard investigated (apple and pear) or tree species (lime and maple).

3. RESULTS

Tables 2, 3, 4 and 5 show the results obtained in the canopies of the apple and pear orchards. There were a total of 253 Coleoptera species in the canopies of apple trees and 188 Coleoptera species in those of pear trees (Markó et al. 1995). At Nagykovácsi, altogether 14,917 specimens of Coleoptera were collected, of which 756 specimens were leaf beetles; there were 176 Coleoptera species collected, of which 36 were leaf-beetle species (Table 2). The number of leaf-beetle specimens collected in Nagykovácsi in 1990–94 appears in Table 3. The commonest leaf-beetle species in the canopy of conventionally treated pear orchard were *Luperus xanthopoda* (Schrank, 1781), *Phyllotreta atra* (Fabricius, 1775), *Phyllotreta nigripes* (Fabricius, 1775) and *Phyllotreta vittula* (Redtenbacher, 1849). In the abandoned apple orchards, the commonest was *L. xanthopoda*, while in the untreated pear orchard, the commonest were *L. xanthopoda*, *Smaragdina (Monrosia) salicina* (Scopoli, 1763) and *Orsodacne lineola* (Panzer, 1794). The high proportion of *L. xanthopoda* in all orchards was probably due to the large number of wild cherry trees in the surrounding mixed oak forest. It is interesting that the number of *P. vittula* was high in the conventionally treated pear orchards in the years investigated. This leaf beetle is not a pear-feeding phytophagous species, its diet being restricted to cruciferous plants and grasses (Vig 1998). The reason of its occurrence in the pear canopy is unknown.

Table 2. Number of Coleoptera specimens and species collected in apple and pear-orchard canopies in Nagykovácsi, Hungary (1990–94)

	A	B	C	Total
Total Coleoptera specimens	7,430	4,506	2,981	14,917
Total Coleoptera species	125	95	70	176
No. of Chrysomelidae specimens	168	181	407	756
No. of Chrysomelidae species	24	17	19	36

A = untreated pear (1990–92); B = untreated apple (1990–92); C = conventionally treated pear (1992–4)

Table 3. Number of leaf-beetle specimens collected in apple and pear-orchards in Nagykovácsi, Hungary (1990–94)

Species	**A**	**B**	**C**	**Species**	**A**	**B**	**C**
Altica sp.	–	17	3	*Luperus xanthopoda* (Schrank, 1781)	52	133	57
Altica oleracea (Linnaeus, 1758)	–	–	1	*Orsodacne lineola* (Panzer, 1794)	31	–	1
Aphthona euphorbiae (Schrank, 1781)	3	2	6	*Oulema melanopus* (Linnaeus, 1758)	2	3	5
Cassida (s. str.) *flaveola* Thunberg, 1794	1	–	–	*Pachybrachis tessellatus* (Olivier, 1791)	1	1	–
Cassida *(s. str.)* nebulosa *Linnaeus, 1758*	7	1	1	*Phyllotreta atra* (Fabricius, 1775)	–	1	32
Chaetocnema (Tlanoma) concinna (Marsham, 1802)	–	–	6	*Phyllotreta cruciferae* (Goeze, 1777)	1	1	7
Chaetocnema (Tlanoma) tibialis (Illiger, 1807)	2	–	–	*Phyllotreta diademata* Foudras, 1859	–	–	1
Clytra laeviuscula (Ratzeburg, 1837)	3	–	–	*Phyllotreta nemorum* (Linnaeus, 1758)	2	3	3
Crepidodera aurata (Marsham, 1802)	–	–	1	*Phyllotreta nigripes* (Fabricius, 1775)	3	3	34
Cryptocephalus (s. str.) *hypochaeridis* (Linnaeus, 1758)	1	2	–	*Phyllotreta nodicornis* (Marsham, 1802)	1	–	–
Cryptocephalus (Burlinius) chrysopus Gmelin, 1790	1	3	–	*Phyllotreta undulata* Kutschera, 1860	–	–	1
Cryptocephalus (s. str.) *imperialis* Laicharting, 1781	3	–	–	*Phyllotreta vittula* (Redtenbacher, 1849)	4	–	245
Cryptocephalus (s. str.) *nitidus* (Linnaeus, 1758)	5	–	–	*Psylliodes* (s. str.) *tricolor* Weise, 1888	–	–	1
Cryptocephalus (s. str.) *nitidus* (Linnaeus, 1758)	–	3	–	*Smaragdina (Monrosia) affinis* (Illiger, 1794)	–	1	–
Gastrophysa polygoni (Linnaeus, 1758)	1	–	–	*Smaragdina (Monrosia) aurita* (Linnaeus, 1767)	1	–	–
Labidostomis longimana (Linnaeus, 1761)	1	–	–	*Smaragdina (Monrosia) salicina* (Scopoli, 1763)	31	3	1
Lachnaia sexpunctata (Scopoli, 1763)	6	3	–	*Sphaeroderma testaceum* (Fabricius, 1775)	–	–	1

A = untreated pear (1990–92); B = untreated apple (1990–92); C = conventionally treated pear (1992–4)

Table 4. Number of Coleoptera specimens and species collected in apple-orchard canopies in Kecskemét, Hungary (1992–94)

	A	B	C	D	E	Total
Total Coleoptera specimens	2075	507	474	449	505	4010
Total Coleoptera species	85	54	45	39	46	131
No. of Chrysomelidae specimens	36	24	13	18	16	107
No. of Chrysomelidae species	14	8	5	7	5	19

A = mature, IPM applied; B = mature, conventionally treated with board-spectrum insecticides; C = young, conventionally treated; D = young, IPM applied; E = young, IPM applied

Table 5. Number of Coleoptera specimens and species collected in pear-orchard canopies in Sárospatak, Hungary (1993–4)

	A	B	Total
Total Coleoptera specimens	490	427	917
Total Coleoptera species	31	31	45
No. of Chrysomelidae specimens	8	19	27
No. of Chrysomelidae species	2	5	6

A = conventionally treated; B = untreated and IPM applied

Table 6. Number of Coleoptera specimens and species and number and proportion of leaf-beetle specimens and species collected in lime and maple canopies in Keszthely, Hungary (1999–2002)

	A	B	Total
Total Coleoptera specimens	4054	2404	6458
Total Coleoptera species	182	211	283
No. (proportion) of Chrysomelidae specimens	266 (6.6%)	441 (18.3%)	707 (10.94%)
No. (proportion) of Chrysomelidae species	31 (17.0%)	45 (21.3%)	53 (18.73)

A = lime; B = maple

At Kecskemét, altogether 4010 Coleoptera specimens were collected of which 107 specimens were leaf beetles and there were 131 Coleoptera species collected of which 19 leaf beetle species were captured (Table 4.). Interestingly, *P. vittula* dominated in both the conventionally and selectively insecticide-treated apple orchards at the end of June and in mid-July in the years investigated.

At Sárospatak, altogether 917 Coleoptera specimens were collected, of which 27 specimens were leaf beetles. There were 45 Coleoptera species represented, including six leaf-beetle species (Table 5).

Table 6 summarizes the results obtained during the investigation of the canopies of lime and maple trees in Hungary. There were a total of 182 Coleoptera species in the lime canopies and 211 Coleoptera species in the maple. At Keszthely, altogether 6458 Coleoptera specimens were collected, of which 707 specimens were leaf beetles. Of the 283 Coleoptera species collected, 53 were leaf-beetle species. The commonest leaf beetle species in the lime canopy were *Aphthona euphorbiae* (Schrank, 1781), *Chaetocnema (Tlanoma) tibialis* (Illiger, 1807), *Longitarsus* (s. str.) *lycopi* (Foudras, 1860), *Longitarsus* (s. str.) *pellucidus* (Foudras, 1860), *Longitarsus* (s. str.) *pratensis* (Panzer, 1794) and *Longitarsus* (s. str.) *succineus* (Foudras, 1860), and in the maple canopy *A. euphorbiae*, *Chaetocnema (Tlanoma) concinna* (Marsham, 1802), *C. tibialis*, *L. lycopi*, *L. pellucidus*, *L. succineus*, *Phyllotreta cruciferae* (Goeze, 1777) and *P. vittula* (Table 7).

The results of metric ordinations show clear differences between the treatments and tree families. The composition (species composition and relative abundance) of leaf-beetle assemblages in the canopies of untreated apple and pear trees was very similar and distinct from the

Table 7. Number of leaf-beetle specimens collected in lime and maple canopies in Keszthely, Hungary (1999–2002)

Species	A	B	Species	A	B
Altica oleracea (Linnaeus, 1758)	–	7	*Longitarsus* (s. str.) *lewisii* (Baly, 1874)	1	2
Aphthona abdominalis (Duftschmid, 1825)	–	2	*Longitarsus* (s. str.) *luridus* (Scopoli, 1763)	7	10
Aphthona euphorbiae (Schrank, 1781)	12	15	*Longitarsus* (s. str.) *lycopi* (Foudras, 1860)	19	24
Aphtona nonstriata (Goeze, 1777)	–	1	*Longitarsus* (s. str.) *melanocephalus* (De Geer, 1775)	–	1
Aphthona semicyanea Allard, 1859	–	1	*Longitarsus* (s. str.) *nasturtii* (Fabricius, 1792)	8	7
Aphthona venustula (Kutschera, 1861)	2	2	*Longitarsus* (s. str.) *pellucidus* (Foudras, 1860)	29	38
Cassida (Mionychella) hemisphaerica Herbst, 1799	–	3	*Longitarsus* (s. str.) *pratensis* (Panzer, 1794)	10	11
Cassida (Hypocassida) subferruginea Schrank, 1776	1	1	*Longitarsus* (s. str.) *rubiginosus* (Foudras, 1860)	–	5
Chaetocnema (s. str.) *aridula* (Gyllenhal, 1827)	–	1	*Longitarsus* (s. str.) *substriatus* Kutschera, 1863	1	3
Chaetocnema (Tlanoma) concinna (Marsham, 1802)	7	14	*Longitarsus* (s. str.) *succineus* (Foudras, 1860)	35	34
Chaetocnema (s. str.) *hortensis* (Geoffroy, 1785)	–	7	*Neocrepidodera ferruginea* (Scopoli, 1763)	2	6
Chaetocnema (Tlanoma) picipes Stephens, 1831	5	10	*Phyllotreta astrachanica* Lopatin, 1977	1	6
Chaetocnema (Tlanoma) tibialis (Illiger, 1807)	17	77	*Phyllotreta cruciferae* (Goeze, 1777)	9	17
Chrysolina (Menthastriella) herbacea (Duftschmid, 1825)	–	1	*Phyllotreta diademata* Foudras, 1859	–	6
Clytra laeviuscula (Ratzeburg, 1837)	–	2	*Phyllotreta nemorum* (Linnaeus, 1758)	–	1
Crepidodera aurata (Marsham, 1802)	2	3	*Phyllotreta nigripes* (Fabricius, 1775)	3	10
Cryptocephalus (Burlinius) planifrons Weise, 1882	1	–	*Phyllotreta procera* (Redtenbacher, 1849)	3	7
Cryptocephalus (s. str.) *sericeus* (Linnaeus, 1758)	1	–	*Phyllotreta striolata* (Fabricius, 1803)	–	1
Epitrix pubescens (Koch, 1803)	2	3	*Phyllotreta undulata* Kutschera, 1860	1	5
Galeruca (s. str.) *pomonae* (Scopoli, 1763)	–	1	*Phyllotreta vittula* (Redtenbacher, 1849)	5	22
Longitarsus sp. 1	–	1	*Psylliodes* (s. str.) *chrysocephalus* (Linnaeus, 1758)	2	7
Longitarsus sp. 2	1	–	*Psylliodes* (s. str.) *illyricus* Leonardi & Gruev, 1993	–	1
Longitarsus (s. str.) *kutscherae* (Rye, 1872)	2	1	*Psylliodes* (s. str.) *napi* (Fabricius, 1792)	1	1
Longitarsus (s. str.) *lateripunctatus personatus* Weise, 1893	2	1	*Psylliodes* (s. str.) *picinus* (Marsham, 1802)	–	1

A = lime (1999–2001; B = maple (1999–2002)

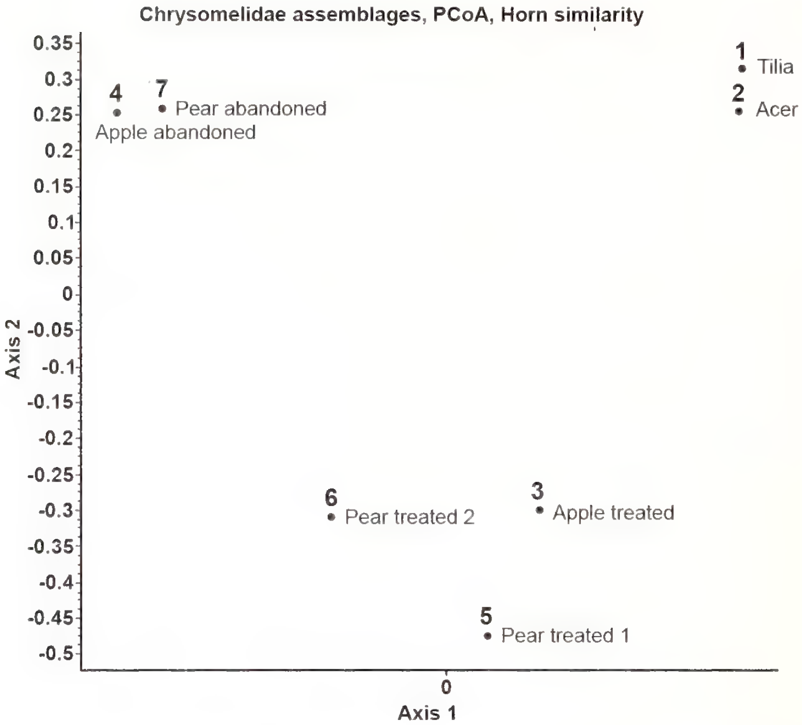

Fig. 1. Examination of the similarity of leaf-beetle assemblages gathered on various deciduous trees, by metric ordination (Horn index).

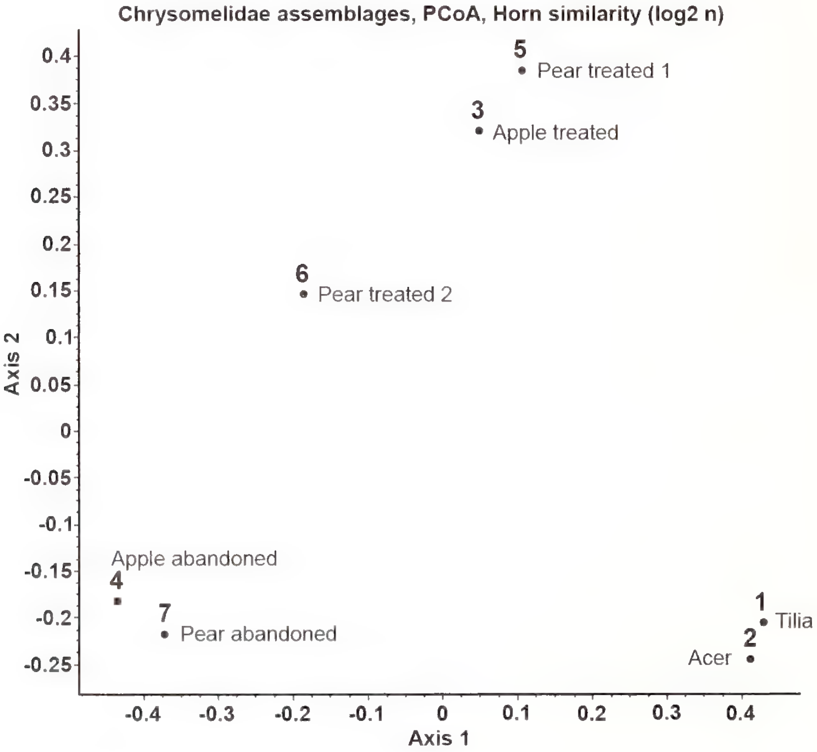

Fig. 2. Examination of the similarity of leaf-beetle assemblages gathered on various deciduous trees, by metric ordination (Horn index, after log2 (x+1) transformation of the raw data).

assemblages of maple and lime trees (Fig. 1). However, the abandoned orchards were situated in the same district (Nagykovácsi) and the maple and lime trees in a different one (Keszthely). It can also be seen that characteristic chrysomelid assemblages were formed in commercial orchards, regardless of differences in their surroundings. On the other hand, the commercial pear orchard2 (No. 6 in the figures) is clearly distinct from the abandoned orchards, despite all being situated in the same district (Fig. 1). The results are similar if the analysis based on log2 transformed data are compared, or only the species compositions (Jaccard index). In these analysis, the role of the commonest, dominant species was lower (log2 transformation) or relative abundance was not taken into consideration (Jaccard similarity) in the comparisons (Figs. 2 and 3). So the results show the basic structure of the chrysomelid assemblages. The neighbouring habitats seem to be more important in forming the species composition of the chrysomelid assemblages. The species composition in the commercial pear orchard2 was closer to the abandoned ones from the same location than to the other commercial orchards. Similarly, the leaf beetle assemblages in the canopies of lime and maple trees from the same location, Keszthely show remarkably similar composition (Fig. 3).

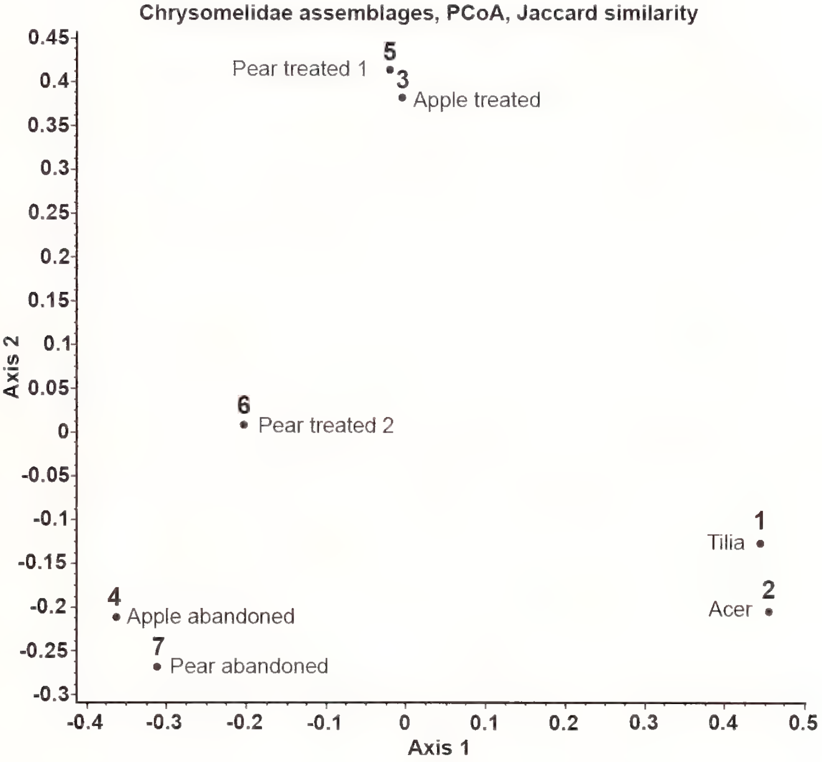

Fig. 3. Examination of the similarity of leaf-beetle assemblages gathered on various deciduous trees, by metric ordination (Jaccard index).

4. DISCUSSION

The leaf-beetle assemblages examined consist of species that sometimes feed on the tree species concerned and much larger specimen and species numbers of visiting species. The untreated apple and pear orchards typically had large numbers of specimens of species feeding on the trees *(L. xanthopoda* and *O. lineola)*. Treatment obviously increases the proportion in the assemblages of visiting species less tied to a food plant (principally and sometimes exclusively *Phyllotreta vittula*), and this causes the distinction in the commercial plantations. On lime and maple species, however, visiting species were found almost exclusively, so that the different characteristics of the two species of tree do not give them distinct beetle faunas. The tourists have a decisive role in species composition. The relatively large number of tourist species (*A. euphorbiae*, *Cassida* (s. str.) *nebulosa* Linnaeus, 1758, *C. concinna*, *Cryptocephalus* (s. str.) *nitidus* (Linnaeus, 1758), *Lachnaia sexpunctata* (Scopoli, 1763), *Oulema melanopus* (Linnaeus, 1758), *P. atra*, *P. cruciferae*, *Phyllotreta nemorum* (Linnaeus, 1758), *P. nigripes*, *P. vittula* and *S. (M.) salicina* in Nagykovácsi and 283 species in the case of Keszthely) have arrived from the environs, so that the species composition is more similar on trees found in the same environment. The explanation for this, as said earlier, is that the environs of the trees have the decisive effect on the development of the species composition.

Leaf beetles contribute a high proportion of the biodiversity of the deciduous tree canopy, sometimes occurring with high species richness and abundance. However, the reasons for this occurrence and their potential role are poorly understood. Most of the species are certainly tourists, which arrived in the canopy by chance, since these tree species are not their food plant. However, it cannot be ruled out that some species may occasionally draw moisture from the leaves of the deciduous tree species examined, especially if the main food plant has become inedible. With some species, consumption of honeydew or sooty moulds is conceivable, although unsupported by observations specific to these species.

Acknowledgements. Károly Vig was supported by the János Bolyai Foundation of the Hungarian Academy of Sciences.

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